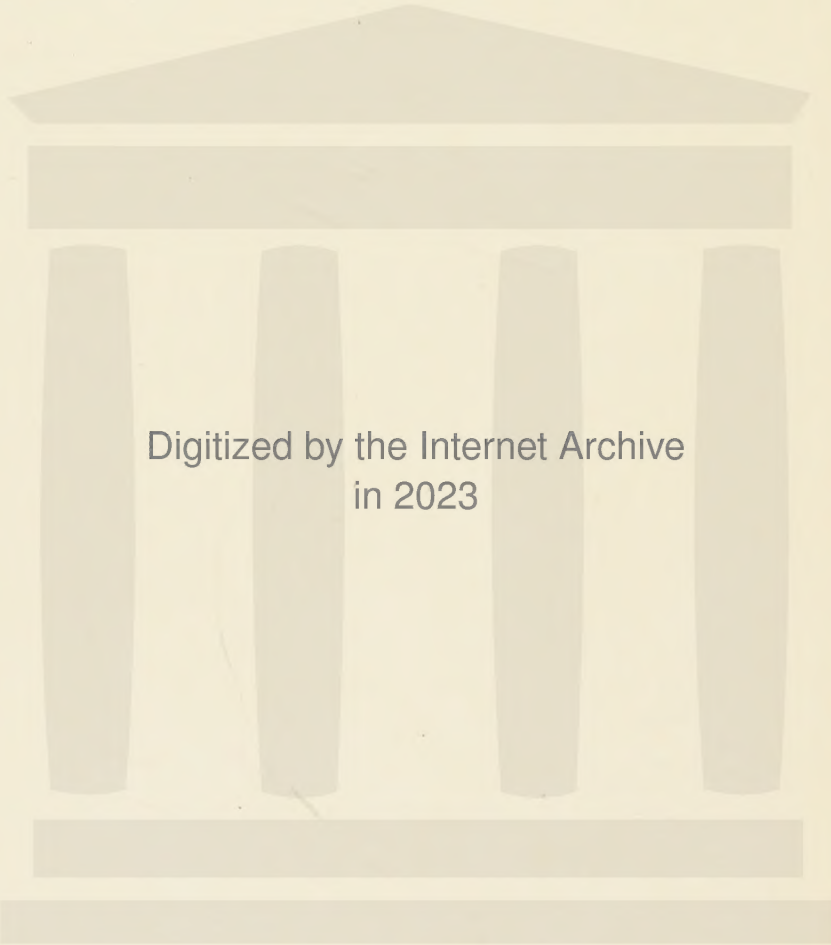




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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

ERRATA

Flora of Panama, Part II. Fasc. 3 (pp. 1-172)—The italicized page numbers at the bottom of the pages should have started with (*309*). However, they should not be changed as they are correct for the Index of Part II.

Page 299, third line, right-hand column of Index—change *grandiflora* to *grandiflora*.

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of the
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FLORA OF PANAMA

Part II. Fascicle 3

ARACEAE

By PAUL C. STANDLEY

Terrestrial or epiphytic plants, very rarely aquatic, herbaceous or often with elongate, suffrutescent caudices, frequently scandent by aerial roots, the terrestrial forms sometimes with tuberous roots, the caudices usually simple but sometimes branched, the foliage glabrous or very rarely pubescent, the sap watery or milky, often caustic; leaves solitary or few in the tuber-bearing plants, in caulescent ones alternate and distichous, or spirally arranged, very variable in form; cataphylls usually present, these narrow, membranaceous, often carinate, sheathing the peduncles or petioles; peduncles simple, terminal or axillary; flowers small, perfect and all alike or unisexual, arranged upon a cylindric, usually elongate spadix, this subtended by a spathe, the spathe various in form, persistent or deciduous, often colored; pistillate flowers, in unisexual plants inserted on the lower part of the spadix, the staminate on the upper portion; perianth usually none in the unisexual flowers, in the perfect flowers of 4-6 segments, these cuneate or obovate, truncate or incurved at the apex, imbricate or rarely connate; stamens in the perfect flowers 4-8 and distinct, hypogynous, opposite the perianth segments, the filaments dilated, the anthers terminal, dehiscent by dorsal pores or slits; stamens of the unisexual flowers 1 to many, distinct or united to form a peltate, prismatic, or sinuate synandrium truncate at the summit; ovary entire or very rarely lobate, sessile or immersed in the spadix, 1- to many-celled; style none, or short or elongate, terminal, simple, the stigma terminal, discoid, pulvinar, or capitate, sometimes sessile along the apex of the ovary and linear-oblong or rarely lobate; ovules solitary or numerous in each cell, sessile or affixed by a short or elongate funicle; fruits baccate, numerous in each spadix, free or connate, indehiscent, or suboperculate by the separation of the thickened apex, the cells usually filled with glutinous or mucilaginous pulp; seeds small or large, smooth or variously roughened, the endosperm commonly abundant and fleshy, rarely none.

The family is essentially a tropical one, abundantly represented in almost all warmer parts of America. A few genera besides those listed here are known from Central America. The group is a well-marked one, whose flower structure may be studied most conveniently, perhaps, in the common calla, *Zantedeschia aethiopica* (L.) Spreng., grown as commonly in Central America as in the United States. A noteworthy feature of the family is the presence in the foliage of

needle-like crystals of calcium oxalate. If a piece of a leaf is chewed, these crystals penetrate the tongue, producing a burning sensation and swelling, the irritation sometimes persisting for many hours.

Most of the Panama Araceae are epiphytic plants, and they form a large percentage of the more conspicuous epiphytic vegetation upon trees of the humid lowlands, being rivaled in abundance only by the bromeliads. The foliage often is handsome and ornamental, and the inflorescences of many species are showy. While most of the plants thrive best in shade, their succulent leaves enable them to live in abundant sunshine. The literature of the Araceae is very extensive, chiefly because they have long been favorite plants in European hot-houses. The most recent and by far the most comprehensive monograph is that of Engler and Krause, *Pflanzenreich* IV. 23. Upon this the following treatment is based. In Central America the family is still but incompletely known, for lack of adequate herbarium material. The plants are succulent and difficult to dry and consequently are neglected by collectors. Moreover, although plants of a given species may be abundant, often it is difficult to find one with inflorescences. It may be stated that when named material is available for comparison, usually it is possible to name specimens from leaves alone.

A study of the development or life history of the Panama plants of the family would be instructive and useful from several aspects. Especially in such genera as *Monstera* and *Philodendron*, the juvenile and adult forms are so different that at first glance one never would associate them. The connecting forms are known or described in but few instances, therefore it often is impossible with present knowledge to name juvenile plants, although it is probable that all of them could be named if their variations were described.

The following key to genera has been prepared with the idea of making it practical rather than diagnostic by the technical characters, which often are difficult of recognition.

- a. Plants aquatic, floating on the surface of water; leaves spongy, arranged in a basal rosette; inflorescence minute and scarcely visible..... 1. *PISTIA*
- aa. Plants terrestrial or epiphytic; leaves not spongy, never arranged in a rosette; inflorescence large and conspicuous.
 - b. Leaves peltate, spotted with white or various colors. Plants terrestrial, naturalized; flowers unisexual, naked..... 7. *CALADIUM*
 - bb. Leaves not peltate, green.
 - c. Leaf blades perforated, sometimes also pinnatifid. Flowers perfect. 4. *MONSTERA*
 - cc. Leaf blades not perforated.
 - d. Leaves digitately compound, pedately 3- to 11-cleft, pinnatifid, or trilobate almost or quite to the base.
 - e. Blades two or more times divided, with very numerous small segments. Plants terrestrial; leaf 1; flowers perfect, with a perianth..... 6. *DRACONTIUM*
 - ee. Blades only once divided or cleft.
 - f. Leaves pinnatifid. Plants epiphytic, with elongate caudices; perianth none.
 - g. Flowers perfect, the spadix uniform..... 4. *MONSTERA*
 - gg. Flowers unisexual, the upper part of the spadix with staminate flowers, the lower with pistillate..... 15. *PHILODENDRON*
 - ff. Leaves trilobate, trisect, or pedately or digitately 5- to 11-parted.

- g. Spathe spreading from the base of the spadix; flowers with a perianth..... 2. ANTHURIUM
- gg. Spathe, at least the lower portion, enclosing the spadix; perianth none.
 - h. Leaves triparted or trisect. Plants epiphytic, with elongate caudices.
 - i. Blades triparted to the base..... 15. PHILODENDRON
 - ii. Blades trisect almost to the base..... 14. SYNGONIUM
 - hh. Leaves pedately cleft, with 5 or more segments.
 - i. Plants terrestrial, arising from a tuberous caudex..... 8. XANTHOSOMA
 - ii. Plants epiphytic, with elongate caudices..... 14. SYNGONIUM
- dd. Leaves simple and entire, often cordate or hastate-lobate at the base.
 - e. Flowers all or mostly perfect, the spadix uniform, not divided into a pistillate and a staminate portion.
 - f. Plants terrestrial, acaulescent.
 - g. Leaf blades acute to rounded at the base..... 5. SPATHIPHYLLUM
 - gg. Leaf blades hastate, with elongate basal lobes..... 3. UROSPATHA
 - ff. Plants epiphytic, at least normally so, usually with a well-developed caudex.
 - g. Stigma discoid; plants with short or elongate caudices.... 2. ANTHURIUM
 - gg. Stigma oblong or linear; plants with elongate, scandent caudices.
 - h. Peduncles cernuous or recurved at the apex at or before anthesis..... 13. STENOSPERMATION
 - hh. Peduncles erect at the apex.
 - i. Lateral nerves of the leaves reticulately anastomosing, the secondary and tertiary ones not parallel with the primary ones..... 4. MONSTERA
 - ii. Lateral nerves of the leaves all more or less parallel, not anastomosing.
 - j. Ovary 2-celled..... 10. RHODOSPATHA
 - jj. Ovary 2- to 6-celled..... 12. ANEPSIAS
 - ee. Flowers unisexual, the spadix with two distinct portions, the lower pistillate, the upper staminate. Perianth none.
 - f. Plants epiphytic, at least normally so, the caudices more or less elongate and rooting at the nodes..... 15. PHILODENDRON
 - ff. Plants terrestrial, acaulescent, or with erect caudices supported by prop roots.
 - g. Leaf blades chiefly oblong, rounded to very shallowly cordate at the base..... 9. DIEFFENBACHIA
 - gg. Leaf blades hastate or cordate, with a deep basal sinus.
 - h. Plants glabrous.
 - i. Caudex erect, usually prickly and supported by prop roots..... 16. MONTRICHARDIA
 - ii. Caudex hypogean, tuberous..... 8. XANTHOSOMA
 - hh. Plants pubescent.
 - i. Stamens distinct..... 11. HOMALONEMA
 - ii. Stamens connate to form a 5- to 6-angulate synandrium..... 8. XANTHOSOMA

1. PISTIA L.

PISTIA L. Sp. Pl. 963. 1753.

Plants aquatic, floating on quiet water, acaulescent or nearly so, the caudex very short, often emitting stolons with new rosettes of leaves at their end, these later becoming detached from the parent plant; leaves numerous, crowded, spirally arranged and forming a rosette, thick and spongy, covered on both surfaces with short, crowded, few-celled hairs; stipular sheath free almost to the base, thin and

scarious; inflorescences very small and inconspicuous, subsessile; spathes foliaceous, whitish, glabrous within, pilose outside, somewhat constricted at the middle on either side, the margins connate to the middle, the blade ovate, acute, subcucullate; spadix shorter than the spathe, adnate for two-thirds its length to the spathe, the pistillate portion 1-flowered, the staminate 2- to 8-flowered, the flowers verticillate; flowers unisexual, naked; staminate flower with 2 stamens, these short-connate, forming a sessile, oblong-ovoid synandrium slightly depressed at its apex, the anther cells opening each by 2 vertical slits; ovary monogynous, ovoid, obliquely attached to the spadix, 1-celled; ovules numerous, orthotropous, sessile, 4- to 6-seriate; style short, terminal, the stigma obtuse, subhemispheric-penicillate; fruit baccate, ovoid, many- or few-seeded, irregularly rupturing; seeds cylindroid, slightly attenuate at the base, subtruncate at the apex, excavate at the middle; endosperm copious.

The genus consists of a single species, almost pantropic in distribution. In general appearance, as well as in structure, the plant is quite unlike any other member of the Araceae, and it constitutes a separate subfamily, Pistioideae. The morphology is discussed in detail by Engler, *Pflanzenreich* IV. 23F:250-258, fig. 63, 64. 1920.

1. *PISTIA STRATIOTES* L. Sp. Pl. 963. 1753.

Plants emitting numerous long, slender roots; primary leaves rounded or broadly obovate, the adult ones numerous, spreading to form a dense rosette, obovate-cuneate or obovate-oblong, broadly rounded or emarginate at the apex, cuneately narrowed to the rather broad, sometimes subpetiolate base, mostly 5-10 cm. long and 2-5 cm. wide, with 5-15 parallel nerves, these prominent beneath, the blades green or grayish green on the upper surface, pale beneath.



Fig. 73. *Pistia Stratiotes*

Generally distributed in tropical regions of the earth except (according to Engler) Polynesia and Micronesia, floating on the surface of quiet pools or streams, and often completely covering the surface of small pools.

Common in the lowlands throughout Panama, chiefly at 100 meters or less.

The English name is "Water Lettuce;" the most common Spanish name of Central America *Lechuga de Agua*, but others are *Lechuga de Sapo*, *Repollo de Agua*, and *Verdolaga de Agua*. The plant often is grown in aquaria in the North.

2. ANTHURIUM Schott

ANTHURIUM Schott, Wien. Zeitschr. Kunst 3:828. 1829.

Plants almost always epiphytic, rarely terrestrial and then perhaps only by accident, the caudex short or sometimes elongate and subscandent, the internodes short or elongate; petioles short or elongate, short-vaginate at the base, always geniculate near the apex; blades usually coriaceous or thick-coriaceous, rarely thin, very variable in form, simple or rarely digitately compound; peduncles commonly elongate, the spathe generally persistent, often colored, narrow, spreading from the base of the spadix, often decurrent at the base; spadix sessile or stipitate, cylindric, conoid, or caudiform, densely many-flowered, usually green or violaceous green, more or less elongate in fruit, flowering from the base upward; flowers perfect, perigoniate; sepals 4, often as broad as long, fornicate above and subtruncate, connivent, somewhat accrescent in fruit; stamens 4, the filaments subcompressed, slightly narrowed into the connective, equaling the sepals, the anthers short, the cells ovate or oblong-ovate, opening by a longitudinal slit; ovary ovoid, oblong, or obovoid, truncate at the apex or attenuate to the style, 2-celled; ovules 2 or 1 in each cell; style none or short, the stigma small, discoid, suborbicular or oblong, subbilobate; berries succulent and juicy at maturity, variously colored, 2-celled, the cells usually 1-seeded; seeds oblong, plane or convex, somewhat attenuate to the apex.

The largest genus of the family, with 500 or more species, all American. They are most numerous in the Andes of northern South America, but 70 or more have been recorded for Central America. The group is a well-marked one, and most of the Central American species can be referred at a glance to it, especially because of the narrow, spreading spathe, and the uniform spadices with only perfect flowers. Many of them are handsome plants, and some are cultivated for ornament locally or even in North America and Europe.

The genus as represented in Panama is a somewhat difficult one, chiefly on account of the large number of species and the quite inadequate material by which they are represented in herbaria. The following treatment is by no means satisfactory, but it is probably the best that can be prepared with the collections now at hand for study. Some of the species recognized are probably not valid, and there are perhaps others represented by imperfect specimens examined.

- | | |
|---|--------------------------|
| a. Leaves pedately parted or deeply trilobate. | |
| b. Leaves merely deeply trilobate..... | 3. <i>A. GARAGARANUM</i> |
| bb. Leaves pedately parted. Large, epiphytic vines. | |
| c. Leaf segments entire..... | 1. <i>A. AEMULUM</i> |
| cc. Leaf segments lobate or undulate..... | 2. <i>A. HOLTONIANUM</i> |
| aa. Leaves entire, but often cordate or hastate at the base and with basal or posterior lobes. | |
| b. Leaf blades deeply cordate or hastate at the base, with large and well-developed posterior lobes, much the broadest at or near the base. | |
| c. Blades conspicuously triangular in outline, the lateral margins shallowly or deeply constricted above the basal lobes. | |
| d. Spadix borne on a stipe 5-15 mm. long..... | 4. <i>A. OCHRANTHUM</i> |
| dd. Spadix sessile or nearly so. | |

- e. Leaves coriaceous, the nerves stout and very conspicuous..... 5. *A. DENUDATUM*
- ee. Leaves membranaceous (when dried), the nerves slender and not markedly conspicuous..... 6. *A. TRIANGULUM*
- cc. Blades ovate or rounded-ovate, the lateral margins convex, nowhere constricted.
 - d. Basal sinus of the blade shallow, much broader than long; blades very thin, the lateral nerves united to form a slender but very distinct collective nerve close to the margin.
 - e. Spadix about 9 cm. long; blades almost 30 cm. long..... 7. *A. WILLIAMSII*
 - ee. Spadix about 3.5 cm. long; blades 18 cm. long or less..... 8. *A. DAVIDSONIAE*
 - dd. Basal sinus of the blade deep, much longer than broad.
 - e. Spathe large, commonly 16 cm. long, the spadix of about equal length..... 9. *A. CONCINNATUM*
 - ee. Spathe smaller, 12 cm. or less.
 - f. Costa of the leaf emitting 5 or fewer lateral nerves on each side above the basal nerves; peduncles shorter than the petioles..... 10. *A. HOFFMANNII*
 - ff. Costa of the leaf emitting 7 or more lateral nerves on each side above the basal nerves; peduncles about equaling the petioles..... 11. *A. BAILEYI*
 - bb. Leaf blades attenuate to rounded at the base, rarely subcordate or emarginate, but then without well-developed basal lobes and not conspicuously broadened near the base.
 - c. Leaves not 3-nerved, the primary lateral nerves extending almost or quite to the margin, or at least not united to form a definite collective nerve.
 - d. Leaves long-petiolate, the blades truncate or shallowly and openly cordate at the base..... 12. *A. COLONICUM*
 - dd. Leaves short-petiolate, the blades gradually narrowed to the cuneate or attenuate base.
 - e. Uppermost portion of the petiole, above the node, not carinate dorsally.
 - f. Upper node of the petiole about as broad as long..... 13. *A. TETRAGONUM*
 - ff. Upper node of the petiole conspicuously longer than broad.
 - g. Spathe 10-25 cm. long or more..... 14. *A. SCHLECHTENDALII*
 - gg. Spathe 6-7 cm. long..... 15. *A. FATOENSE*
 - ee. Uppermost portion of the petiole, above the node, conspicuously 1- to 5-carinate dorsally.
 - f. Blades chiefly 10-15 cm. wide..... 16. *A. AGNATUM*
 - ff. Blades commonly 25-30 cm. wide or larger.
 - g. Upper node of the petiole 3-carinate..... 17. *A. CRASSINERVIVUM*
 - gg. Upper node of the petiole 5-carinate..... 18. *A. MAXIMUM*
 - cc. Leaves evidently 3-nerved, the primary lateral nerves united to form a definite collective nerve close to the margin of the blade.
 - d. Plants normally with well-developed, long caudices having elongate internodes.
 - e. Leaf blades acute at the base, coriaceous, 16 cm. long or less.
 - f. Spadix slender-stipitate; petioles more than half as long as the blades..... 19. *A. PITTIERI*
 - ff. Spadix sessile; petioles mostly less than half as long as the blades.
 - g. Peduncles 2-3 times as long as the petioles..... 20. *A. TRINERVE*
 - gg. Peduncles equaling or slightly exceeding the petioles..... 21. *A. SCANDENS*
 - ee. Leaf blades very obtuse, rounded or even subcordate or emarginate at the base.
 - f. Blades with 2 of the lower lateral nerves much more conspicuous than the others and extending to the apex; spadix conspicuously attenuate upward..... 22. *A. MYOSUROIDES*
 - ff. Blades with all the primary lateral nerves subequal, none of them extending to the apex; spadix very obtuse, not attenuate upward.
 - g. Leaf blades subcordate at the base..... 23. *A. GRACILENS*
 - gg. Leaf blades rounded at the base.
 - h. Spadix almost sessile..... 24. *A. MICROSPADIX*

- hh. Spadix conspicuously stipitate..... 25. *A. PALLENS*
- dd. Plants acaulescent or nearly so, the caudex very short, never with elongate internodes.
 - e. Leaf blades truncate or even subcordate at the base..... 26. *A. TALAMANCAE*
 - ee. Leaf blades long-attenuate to obtuse at the base.
 - f. Blades conspicuously broadest above the middle, oblanceolate to obovate, long-attenuate to the base.
 - g. Leaves thin and almost membranaceous when dried, narrowly long-attenuate at the apex, 6.5 cm. wide or less, the very slender submarginal nerve irregular and more or less crenate.
 - h. Leaf blades less than 5 cm. wide; petiole geniculate near the apex..... 27. *A. SCOLOPENDRINUM*
 - hh. Leaf blades more than 5 cm. wide; petiole geniculate 1 cm. below the apex..... 28. *A. MICHELII*
 - gg. Leaves coriaceous when dried, short-acuminate or abruptly cuspidate-apiculate, 9–20 cm. wide or more, the stout marginal nerve even.
 - h. Node of the petiole 5 mm. thick; blades about 9 cm. wide; spadix in anthesis scarcely 4 mm. thick..... 29. *A. RAMONENSE*
 - hh. Node of the petiole 1 cm. thick or more; blades mostly about 20 cm. wide; spadix in anthesis 1 cm. thick or more..... 30. *A. HACUMENSE*
 - ff. Blades broadest at or below the middle, not very long-attenuate to the base.
 - g. Leaves linear or essentially so, less than 3.5 cm. wide, thick-coriaceous..... 31. *A. GRACILE*
 - gg. Leaves usually conspicuously broader than linear, if almost linear, then not thick-coriaceous, generally much more than 3.5 cm. wide.
 - h. Blades oblong to elliptic-oblong or narrowly elliptic, usually less than 4 times as long as wide, mostly 5–13 cm. wide.
 - i. Petioles much less than half as long as the blades; leaves coriaceous when dried..... 32. *A. LITTORALE*
 - ii. Petioles about half as long as the blades; leaves relatively thin when dried and scarcely coriaceous..... 33. *A. ACUTANGULUM*
 - hh. Blades narrowly oblong or linear-oblong, most of them 5 times as long as wide or longer, mostly 3.5–8 cm. wide, but sometimes somewhat wider.
 - i. Primary lateral nerves of the leaves stout and salient, much more conspicuous than the secondary ones..... 34. *A. JOSEANUM*
 - ii. Primary lateral nerves very slender, scarcely if at all stouter or more prominent than the secondary ones.
 - j. Petioles less than half as long as the blades..... 35. *A. TURRIALBENSE*
 - jj. Petioles almost equaling the blades.
 - k. Leaf blades not punctate..... 36. *A. CHIRIQUENSE*
 - kk. Leaf blades conspicuously punctate on both surfaces..... 37. *A. ALLENII*

1. *ANTHURIUM AEMULUM* Schott, Bonplandia 7:165. 1859.

A large, epiphytic vine, the caudex slender, with elongate nodes; cataphylls caducous; petioles slender, equaling or longer than the blades, geniculate near the apex; blades 7- to 11-parted, the segments sessile or petiolulate, 15–30 cm. long, mostly 5–7 cm. wide, oblong-elliptic or oblanceolate-oblong, thin when dried, cuspidate-acuminate, cuneately narrowed to the base, the lateral nerves united to form 2 collective nerves, one close to the margin, the other remote from it, all the nerves very slender; peduncles 5–15 cm. long, slender or stout; spathe 7–10 cm.



Fig. 74. *Anthurium aemulum*

A. aemulum, but it appears questionable whether the attachment of the leaf segments, i. e., whether they are sessile or stipitate, is an important taxonomic character.

2. *ANTHURIUM HOLTONIANUM* Schott, Oesterr. Bot. Zeitschr. 8:350. 1858.

Usually a very large, scandent epiphyte, the caudex often thick; petioles slender or stout, as much as a meter long, geniculate near the apex, the terete node as broad as long; blades often very large, a meter or more in breadth, 5- to 9-cleft, the segments sessile or nearly so, attenuate at the base, shallowly or deeply lobate or merely undulate, thin when dried, the lateral lobes obtuse or rounded, the terminal lobe of each main segment acuminate; peduncles about 60 cm. long, sometimes shorter; spathes 30–65 cm. long, 3 cm. wide or more, wine-red or dull brick-red, linear-lanceolate, very long-acuminate; spadix caudiform, gray or dark red, 40–80 cm. long, about 2 cm. thick at the base, slightly attenuate upward.

Climbing over trees or rocks in humid forest, at or near sea level, Costa Rica to Colombia.

CANAL ZONE: Barro Colorado Island, *Kenoyer* 178; *Aviles* 26; *Woodworth & Vestal* 554; *Frost* 108; *Shattuck* 280, 762; *Standley* 31452, 41078; Las Cascadas Plantation, near Summit, *Standley* 25708, 25722, 25732, 25750; Fort Randolph, *Standley* 28027; Fort Sherman, *Standley* 31155; Gorgona, *Maxon* 6788. DARIÉN: Boca de Cupe, *Williams* 061. PANAMÁ: La Chorrera, *Paul* 502.

One of the commonest and most showy aroids of the Isthmus region, easy of recognition because of its pedately parted leaves with lobed segments. The earliest leaves of juvenile plants are simple, the next have two or three segments,

long, 1–2.5 cm. wide at the base, lanceolate or linear-lanceolate, pale green; spadix short-stipitate or sessile, conoid or at first caudiform, somewhat attenuate upward, 3–10 cm. long, as much as 13 mm. thick.

Scandent on trees in wet forest, mostly at 250 meters or less, southern Mexico to Panama.

CANAL ZONE: Barro Colorado Island, *Shattuck* 125. COLÓN: *Fató*, *Pittier* 3864. PANAMÁ: Río Tapia, *Standley* 28258.

The plant is a rather handsome and decorative one, easily recognized by its leaf form. In two of the specimens cited the leaf segments are conspicuously stipitate, which would exclude them, according to Engler's key to species, from

At this stage the segments are not at all lobed, and such juvenile plants can be mistaken easily for *P. aemulum*, but the venation is different in the two species.

3. *ANTHURIUM GARAGARANUM* Standl. Field Mus. Bot. Ser. 22:68. 1940.

A large, coarse plant, the caudex apparently short and thick; petioles stout, 40–60 cm. long, narrowly sulcate, subterete, geniculate about 1.5 cm. below the apex, the node 7–8 mm. thick; blades deeply 3-lobate to about 5 cm. above the subtruncate base, the lateral lobes incurved-falcate, 23–36 cm. long, 10–11 cm. wide, obtuse or subacute, rounded on the outer margin, almost straight on the inner margin, the costa dividing about 4 cm. above the base into 4 primary nerves, these stout and extending almost or quite to the apex of the segment, the middle segment 36 cm. long and 9 cm. wide or larger, narrowly long-acuminate, the costa very stout and prominent beneath, the primary costal nerves numerous, rather stout and prominent, divergent at an angle of 45 degrees or more, united to form a rather irregular collective nerve close to the margin; peduncle about 25 cm. long, terete, 5–7 mm. in diameter; spathe lance-linear, 17 cm. long, 1.5 cm. wide near the base; spadix slender, caudiform, sessile or nearly so, 17 cm. long, 9 mm. in diameter near the base, slightly attenuate upward.

Known only from the original Panama collection.

DARIÉN: foothills of Garagará, 30–500 m., Pittier 5601 (TYPE).

The type material was determined by Krause as *Philodendron tripartitum* (Jacq.) Schott, a plant that it does not resemble closely in leaf form. It is clearly an *Anthurium*, and appears related to *A. tripartitum* Engler. This was described from Barbacoas, Colombia, and its description agrees well in some respects with the Panama plant, but certain characters of *A. tripartitum*, as that is described by Engler, make it plain that *A. garagaranum* must be considered distinct.

4. *ANTHURIUM OCHRANTHUM* C. Koch, Ind. Sem. Hort. Berol. App. 16. 1853.
Anthurium lapathifolium Schott, Oesterr. Bot. Wochenbl. 7:309. 1857.

Caudex as much as 1 m. high; petioles 6–9 cm. long, geniculate 2 cm. below the apex, subterete; blade gradually narrowed above the basal lobes to the abruptly narrowed and cuspidate apex, 50 cm. long or more, the basal lobes 15 cm. long and 10 cm. wide, elongate-oblong, with almost equal sides, rounded, the basal sinus triangular or oval, open, the basal nerves 5–6 on each side, the costal nerves 7–9 on each side, united to form a collective nerve remote from the margin; peduncles 1 m. long or more; spathe 20 cm. long, lanceolate, long-acuminate, short-decurrent at the base, green or yellowish green; spadix borne on a stipe 5–15 mm. long, at first violet, later yellow, elongate-fusiform, 20 cm. long, 1 cm. thick; ovaries cylindroid, the style exserted above the sepals; berries ovoid, 1 cm. long, 5 mm. thick, whitish; seeds cordiform, the testa green, verruculose.

Costa Rica and Panama.

CANAL ZONE: Chagres, Fendler 429 (TYPE of *A. lapathifolium*).

I have seen nothing to represent this species, but from description it must be fully distinct from any other species listed here.

5. *ANTHURIUM DENUDATUM* Engler, Bot. Jahrb. 6:280. 1885.



Fig. 75. *Anthurium denudatum*

Plants epiphytic, or sometimes, perhaps accidentally, terrestrial, often very large and coarse, the caudex said to be sometimes a meter long, the internodes short and thick; cataphylls persistent but weathering into long fibers; petioles mostly 60–70 cm. long, geniculate near the apex, the node short and thick; blades thick-coriaceous when dried, hastate-trilobate, 30–50 cm. long or larger, the basal lobes rather narrow and more or less spreading, subreniform, somewhat recurved, separated by a very broad but deep sinus, the anterior lobe lance-oblong or ovate-oblong, acute or acuminate, 8–15 cm. wide below, the primary nerves very stout and salient, the costal nerves united to form an irregular collective nerve remote from the margin; peduncles 20–50 cm. long or more, slender or stout; spathes 7–20 cm. long, as much as 2.5 cm. wide near the base, linear-lanceolate, cuspidate-acuminate, reddish brown or greenish; spadix short-stipitate or almost sessile,

cylindric or caudiform, 14–35 cm. long, in fruit up to 2.5 cm. in diameter at the base; sepals almost 3 mm. long; ovaries ovoid, 2 mm. long, attenuate to a style 1 mm. long; berries orange, 7 mm. long or more.

Panama and Colombia, in the latter country reported to occur at an elevation of 1,800 meters.

CANAL ZONE: near Gatún, *Hayes*; Balboa, cultivated, *Standley* 28559; Río Indio de Gatún, *Pittier*, 2779, 2799; Barro Colorado Island, *Starry* 232; *Kenoyer* 181; *Woodworth & Vestal* 567. COCLÉ: north rim of El Valle, *Allen & Alston* 1844. PANAMÁ: Arenoso, lower Río Trinidad, *Seibert* 598.

Illustrated, *Pflanzenreich* IV. 23B: fig. 71. The species is a well-marked one, its leaf form quite distinctive and easy of recognition when once known.

6. *ANTHURIUM TRIANGULUM* Engler, Bot. Jahrb. 25:383. 1898.

Plants epiphytic or sometimes terrestrial, the caudex short or occasionally elongate, the internodes 1.5 cm. long or less; cataphylls lanceolate, 3–4 cm. long; petioles slender or stout, 30–45 cm. long or more, geniculate 1–2 cm. below the

apex; blades rather thin when dried, triangular-sagittate, mostly 30–40 cm. long and 15–25 cm. wide, the basal lobes separated by a broad, open, shallow or deep sinus, rather narrow or broadly rounded, often directed outward but more often downward, the anterior lobe acute to acuminate and long-cuspidate, the costal nerves 3–4 or more on each side, slender but very prominent, remote, united to form a distinct collective nerve near or remote from the margin; peduncles longer or shorter than the petioles, slender, mostly 25–35 cm. long; spathes linear-lanceolate or lance-oblong, 5–11 cm. long, 1–2.5 cm. wide; spadix gray-green, sessile or nearly so, 5–10 cm. long, stout, but slightly narrowed upward; ovary oblong, 3 mm. long, 1.5 mm. thick; berries 3.5 mm. long, 2.5 mm. thick, maroon.

Humid forest, at or near sea level, Panama and Costa Rica (?).

CANAL ZONE: Gamboa, *Standley* 28398, 28399; Frijoles, *Standley* 27567; Río Indio de Gatún, *Pittier* 2795; Barro Colorado Island, *Standley* 31286, 41044, 41087; *Kenoyer* 190; *Aviles* 17. BOCAS DEL TORO: Isla Colón, Chiriquí Lagoon, *Wedel* 122; Shepherd Island, Chiriquí Lagoon, *Wedel* 2720 (TYPE from Shirores, Talamanca, Costa Rica, *Pittier* & *Tonduz* 9225).

7. *ANTHURIUM WILLIAMSII* Krause, Notizbl. Bot. Gart. Berlin 11:610. 1932.

Plants apparently epiphytic, the stout caudex 1.5 cm. thick, the internodes short; cataphylls linear-lanceolate, acute, about 8 cm. long, soon weathering into fibers; petioles very slender, 50–60 cm. long, geniculate 1 cm. below the apex, the node relatively slender; blades thin and membranaceous when dried, broadly ovate in outline, acute or short-acuminate, cordate at the base and somewhat unequal, the basal sinus broadly triangular and open, sometimes 5 cm. deep, the basal lobes broadly rounded, directed downward, the blade about 28 cm. long and 20 cm. wide, the primary lateral nerves 14–16 on each side, very slender, prominulous on both sides, ascending at a wide angle, united to form a slender collective nerve 3–5 mm. from the margin; peduncles slender, terete, 20 cm. long; spathe green, oblong-lanceolate, acuminate, 4 cm. long, 1 cm. wide; spadix subsessile, dark red, narrowly cylindric, obtuse, caudiform, 9 cm. long, 4–5 mm. thick; sepals oblong, 1.5 mm. long; pistils ovoid.

Known only from the original collection, from Panama.

DARIÉN: Cana, 600–1950 m., *Williams* 817 (TYPE).

8. *ANTHURIUM DAVIDSONIAE* Standl. Field Mus. Bot. Ser. 22:4. 1940.

Plants said to be terrestrial, but appearing to be essentially epiphytic, the caudex slender and elongate, about 6 mm. thick, with short internodes; cataphylls linear-attenuate, as much as 12 cm. long, the nodes emitting numerous long roots; petioles very slender, 12–19 cm. long, geniculate about 1 cm. below the apex, the node very slender; blades ovate-oval or broadly oval, membranaceous when dried, 15–18 cm. long, 9.5–11 cm. wide, obtuse at the apex and abruptly caudate-acuminate, with an acumen 2 cm. long or more, broadly and shallowly cordate at the base, the basal lobes broadly rounded, the basal sinus much broader than deep, slightly paler beneath, 9-nerved at the base, the primary costal nerves about 12



Fig. 76. *Anthurium Davidsoniae*

broadly ovate-cordate or deltoid-cordate, mostly 40–50 cm. long and almost as wide, cuspidate-acuminate, the basal lobes one-third as long as the posterior one or shorter, broadly rounded, separated by a deep and rather narrow but open sinus, directed downward or somewhat incurved, the primary costal nerves 5 or more on each side, stout and very prominent, united to form a prominent collective nerve close to the margin; peduncles 50 cm. long or more; spathe lanceolate, 15–18 cm. long, 3–4 cm. wide near the base, acuminate; spadix subsessile or on a stipe 1 cm. long, often 18 cm. or more in length, dark red at first, 1 cm. thick below, somewhat attenuate upward; sepals linear; ovaries oblong, gradually attenuate to a thick, conoid style.

Humid forest, Panama and Costa Rica, and probably extending to Honduras or even farther northward.

CHIRIQUÍ: Bajo Chorro, Boquete District, 1800 m., *Davidson 284, 405*; trail from Cerro Punta to headwaters of Rio Caldera, 2250–2500 m., *Allen 1453*; Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m., *Woodson & Schery 382*. BOCAS DEL TORO: reported from Shirores, Talamanca, 100 m., *Pittier & Tondus 9230*. COCLÉ: north rim of El Valle de Antón, near Cerro Turega, 700 m., *Woodson & Schery 194*.

on each side, ascending at an angle of about 45 degrees, very slender, united to form a distinct collective nerve remote from the margin; peduncles slender, 9–11 cm. long; spathe pale green, narrowly oblong, 3 cm. long and 5 mm. wide, long-acuminate; spadix pale yellow, sessile, obtuse, 2.5–3.5 cm. long, 3–4 mm. thick, slightly attenuate upward.

Known only from Chiriquí, Panama.

CHIRIQUÍ: in rain forest, Bajo Chorro, Boquete District, 1800 m., *Davidson 134* (TYPE); vicinity of Bajo Chorro, 1900 m., *Woodson & Schery 691*.

9. *ANTHURIUM CONCINNATUM* Schott,
Prodr. Aroid. 522. 1860.

Anthurium bogotense Schott var. *concinatum*
Engler in DC. Monogr. Phan. 2:184. 1879.

Plants usually epiphytic but reported to be sometimes terrestrial, the caudex short or elongate, as much as 2 cm. thick, the internodes usually short; cataphylls narrowly oblong, often persistent and rather thick; petioles slender, mostly 40–60 cm. long, geniculate about 2 cm. below the apex; blades subcoriaceous when dried,

10. *ANTHURIUM HOFFMANNII* Schott, Oesterr. Bot. Zeitschr. 8:181. 1858.*Anthurium tsakianum* Engler, Bot. Jahrb. 25:423. 1898.Fig. 77. *Anthurium Hoffmannii*

Plants epiphytic or terrestrial on rocky banks, the caudex often assurgent and 30 cm. long or more, as much as 2 cm. thick, with short internodes; cataphylls 10–16 cm. long, linear-oblong, persistent and rather coriaceous, brown when dried; petioles slender or stout, 40–60 cm. long, geniculate 2–3 cm. below the apex; blades subcoriaceous when dried, broadly ovate-cordate, mostly 25–35 cm. long and 20–25 cm. wide, shortly cuspidate-acuminate, the posterior lobes broadly rounded, directed downward or slightly inward, the sinus open but usually narrow, the primary costal nerves 3–4 on each side or rarely more, rather stout and prominent beneath, united to form a distinct collective nerve rather remote from the margin; peduncles 15–30 cm. long; spathes lanceolate, commonly 8–10 cm. long and 2–3 cm. wide, long-acuminate or caudate-acuminate, whitish or greenish; spadix sessile or short-stipitate, cylindric, obtuse, dark red, 6–12 cm. long, almost 1 cm. thick at the base or in fruit 1.5 cm.; fruits red.

Usually on trees, sometimes on rocky banks, humid forest, mostly at 250–3000 m., Panama and Costa Rica.

CHIRIQUÍ: Bajo Mono, Boquete District, *Davidson 461*; Finca Lérída to Boquete, *Woodson, Allen & Seibert 1170*; near El Boquete, *Pittier 2872, 2965*; Volcán de Chiriquí, 3000 m., *Davidson 986*. COCLÉ: north rim of El Valle, *Allen & Alston 1845*; floor of El Valle, *Allen 2230*. BOCAS DEL TORO: Tsaki, Talamanca, *Tonduz 9510* (TYPE of *A. tsakianum*); seven miles north of Bocas del Toro, *Wedel 344*.

11. *ANTHURIUM BAILEYI* Standl. Field Mus. Bot. Ser. 22:66. 1940.

Plants rather large and coarse, terrestrial, the caudex very short or almost none, about 1.5 cm. thick, with very short internodes; cataphylls short, more or less withering-persistent; petioles 50–60 cm. long, rather slender, 7 mm. thick near the base, terete, brownish when dried; blades deltoid-ovate-cordate, thin and almost membranaceous when dried, about 44 cm. long and 32 cm. wide, abruptly short-acuminate, green above and usually densely black-punctate, somewhat paler beneath, the basal lobes large, rounded or somewhat obtuse-angulate on the outer

margin, making the blade slightly hastate, the sinus broad, open, triangular, 12 cm. deep, the primary costal nerves about 7 on each side, united to form a slender, irregular collective nerve close to the margin, the basal nerves 5; peduncles about 45 cm. long, slender, terete, brownish; spathe apparently green, 12.5 cm. long, 1.5 cm. wide at the base, linear-lanceolate, very long-attenuate, slightly shorter than the spadix; spadix borne on a stipe 1.5 cm. long or more, 12 cm. long, 7–8 mm. thick at the base, slightly attenuate upward, obtuse.

Known only from Panama, in humid forest near sea level.

CANAL ZONE: Barro Colorado Island, L. H. & E. Z. Bailey 196 (TYPE); Standley 31294, 41104; hills north of Frijoles, Standley 27440. PANAMÁ: Río Tapia, Standley 26159; Río Tecumen, Standley 26739. SAN BLAS: Puerto Obaldía, Pittier 4277.

Pittier 4277 was determined by Krause as *A. nitidum* Benth., apparently in error. There is some doubt as to whether all the specimens cited represent a single species. In the type specimen, the only one bearing an inflorescence, the petioles are smooth and the blades are glabrous. In several of the other specimens the petioles are aculeolate, and the blades are conspicuously puberulent beneath, at least along the nerves. The plants are common on Barro Colorado Island, and all the leaf specimens probably are conspecific, although it is quite possible that more ample material will show that two distinct species, or even genera, are represented.

12. *ANTHURIUM COLONICUM* Krause, Bot. Jahrb. 54, Beibl. 118:123. 1916.

Plants large and coarse, epiphytic, the caudex apparently short, very thick, with short internodes; petioles half to three-fourths as long as the blades, stout, terete, 40–60 cm. long, 15–18 mm. thick near the base, geniculate 3–3.5 cm. below the apex; blades coriaceous when dried, oblong, 60–80 cm. long, 15–20 cm. wide, somewhat narrowed near the apex and cuspidate-acuminate, truncate or shallowly cordate at the base, with broad, rounded basal lobes, the costa stout and prominent beneath, the primary costal nerves 12–16 on each side, stout and prominent, irregularly anastomosing near the margin but not forming a distinct collective nerve; peduncles rather stout, terete, about 30 cm. long and 8–10 mm. thick; spathe lanceolate, long-acuminate, slightly decurrent upon the peduncle, 10 cm. long and 3 cm. wide; spadix borne on a stipe almost 2 cm. long, narrow-cylindric, slightly attenuate upward, obtuse, 15 cm. long, 1.5 cm. thick at the base; sepals 1.5–1.8 mm. long; pistils ovoid.

Known only from the original Panama collection.

COLÓN: forests about Porto Bello, near sea level, Maxon 5801 (TYPE).

13. *ANTHURIUM TETRAGONUM* Hook. ex Schott, Prodr. Aroid. 475. 1860.

Plants large and coarse, epiphytic, the short caudex 6–8 cm. thick, with very short internodes; petioles scarcely one-sixth as long as the blades, 10–20 cm. long or shorter, broadly canaliculate above, the short node cubical; blades coriaceous when dried, broadly obovate to oblanceolate, 60–130 cm. long and 25–50 cm. wide when well developed, rounded and short-cuspidate at the apex, cuneately narrowed to the base, the costa very thick and subpentagonal, 1–2 cm. thick at

the base, the primary lateral nerves 15–20 on each side, erect-spreading, not united to form a distinct collective nerve, stout and prominent; peduncles terete, one-third as long as the blades or shorter, mostly 20–30 cm. long; spathe oblong-lanceolate, long-cuspidate, obliquely decurrent at the base, 15–20 cm. long, 3–4 cm. wide near the base; spadix short-stipitate, 2–3 cm. thick at the base, caudate-attenuate upward, dull green, 15–25 cm. long; sepals 3 mm. long and one-third as wide; stamens equaling the sepals; ovary subfusiform, half longer than the sepals, attenuate to the apex; berries elongate-turbinate, purplish below, yellowish green toward the apex, 1–1.5 cm. long, 2–3 mm. thick, 1- to 3-seeded; seed oblong, one-third as long as the berry.

Lowland forests of Costa Rica and Panama, and perhaps more widely distributed.

CHIRIQUÍ: David, *Pittier 2844* (determined by Krause). BOCAS DEL TORO: Shirores, Talamanca, *Tonduz 9228, 9234*; Tsaki, *Tonduz 9507* (reported by Engler).

14. *ANTHURIUM SCHLECHTENDALII* Kunth, Enum. Pl. 3:75. 1841.

Plants epiphytic or terrestrial, often growing on rocks, rather large and coarse, acaulescent; petioles subtetragonous, less than one-fourth as long as the blade, usually very short, sometimes as much as 15 cm. long and 1–1.5 cm. thick, with a very short node; blades obovate-oblong or oblanceolate-oblong, commonly 50–60 cm. long and 15–20 cm. wide, often larger, acute or acuminate, coriaceous when dried, gradually narrowed from about the middle to the narrow, cuneate base, the costa stout and prominent, 1 cm. thick at the base, the primary lateral nerves about 14 on each side, stout and prominent, not forming a distinct collective nerve, ascending at an angle of 45 degrees; peduncles shorter than the leaves, often very short, sometimes 60 cm. long, stout or slender; spathe reflexed, 10–25 cm. long or more, 2 cm. wide near the base, pale green or sometimes tinged with red or purple, long-attenuate, more or less decurrent at the base upon the peduncle; spadix 15–25 cm. long, often 1 cm. or more in diameter at the base, attenuate upward, reddish or greenish, in fruit 2 cm. thick.

Humid forest, or sometimes in exposed situations, usually at or near sea level, but in Mexico ascending to 1,000 meters, Panama to Mexico.

CANAL ZONE: Obispo, *Standley 31719*; Barro Colorado Island, *Shattuck 638*; *Standley 31343*; near Gatún, *Standley 27210*; Culebra, *Pittier 2608*; Balboa, cultivated, *Standley 28578*.

It may be remarked here that the species of this alliance, nos. 13 to 18, inclusive, are very much confused, at least in the mind of the writer, and probably not less so by Engler and Krause. Much more material is needed before their proper disposition can be determined satisfactorily. The writer is not at all satisfied with the arrangement of the species made here, and it is probable that errors have been made both in determination and division of the available collections. I have depended largely upon determinations by Krause of plants collected by Pittier during the Smithsonian Biological survey of the Canal Zone, but I do not believe that even those are too dependable.

15. *ANTHURIUM FATOENSE* Krause, Notizbl. Bot. Gart. Berlin 11:611. 1932.

Said to be terrestrial, but probably an essentially epiphytic plant, the caudex terete, short, 1.5 cm. thick, the internodes very short; cataphylls linear, long-attenuate, soon deciduous; petioles stout, 4-7 cm. long, 6-7 mm. thick, canaliculate for their whole length, the node very short, scarcely thickened; blades thin and almost membranaceous when dried, obovate-oblong, 50-65 cm. long, 13-16 cm. wide, long-acuminate, gradually narrowed from above the middle to the attenuate base, the costa rather stout and very prominent, the primary lateral nerves numerous, slender, prominent on both surfaces, arcuately ascending at a rather wide angle, not united to form a distinct collective nerve; peduncles slender, terete, 40-45 cm. long, 4-5 mm. thick; spathe linear-lanceolate, acuminate, 6-7 cm. long, 7 mm. wide; spadix sessile, narrowly cylindric and caudiform, rounded at the apex, 12-14 cm. long, 6-8 mm. thick near the base; sepals oblong, 2 mm. long, 1.2 mm. wide; pistils ovoid; berries oblong-ovoid, attenuate upward, 4-5 mm. long, 2 mm. thick.

Known only from the original Panama collection.

COLÓN: Dos Bocas, Río Fató Valley, 40-80 m., *Pittier 4227* (TYPE).

16. *ANTHURIUM AGNATUM* Schott, Oesterr. Bot. Zeitschr. 8:181. 1858.

Plants epiphytic, large and coarse, acaulescent or nearly so, the caudex short and very thick; petioles one-fourth as long as the blades or shorter, mostly 10-15 cm. long but often shorter, with a short, oblong node; blades coriaceous when dried, oblong-oblancheolate or oblanceolate, 30-50 cm. long and 10-13 cm. wide or sometimes larger, acute or acuminate, gradually long-attenuate from above the middle to the long and narrow, often almost stipe-like base, the costa stout and prominent, the primary lateral nerves few, rather slender, prominent on both surfaces, arcuately ascending at an angle of about 45 degrees, not united to form a distinct collective nerve; inflorescences still imperfectly known.

On trees in humid forest, Panama and Nicaragua.

CANAL ZONE: between Gorgona and Gatún, *Pittier 2278* (determined by Engler); Balboa, cultivated, *Standley 28564*; Fort Sherman, *Standley 31018*. CHIRIQUÍ: Bajo Chorro, Boquete District, *Davidson 276* (determination doubtful).

This species is perhaps too close to *A. Schlechtendalii*.

17. *ANTHURIUM CRASSINERVIVM* (Jacq.) Schott, Melet. 1:22. 1832.

Pothos crassinervia Jacq. Icon. 3: pl. 609. 1793.

Plants normally epiphytic, very large and coarse, the caudex thick and short; petioles usually very short and thick, 3-carinate dorsally, 15-30 cm. long or often shorter, 2-3 cm. in diameter, the node 1.5-2 cm. long, tricarinate dorsally; blades coriaceous when dried, oblong-oblancheolate to obovate, usually 60-100 cm. long and 25-30 cm. wide but often much wider and longer, cuspidate-acute, cuneately long-attenuate to the narrow base, green above, slightly paler beneath, the costa very thick, 3- to 5-angulate, the primary lateral nerves 9-14 on each side, stout, prominent, spreading or erect-patent, not forming a distinct collective nerve;

peduncles shorter than the leaves, as much as 70 cm. long, about 1 cm. thick, angulate below, terete above; spathe subcoriaceous, dark red within, linear-lanceolate, long-acuminate, 12.5 cm. long or even longer, 2.5 cm. wide at the base; spadix short-stipitate, purple when young, later becoming white, caudiform, 15–30 cm. long and 1.5 cm. thick, or in fruit much larger or at least thicker, often 5 cm. or more in diameter, attenuate toward the apex; ovary ovoid, equaling the sepals; berries ovoid, bright red, 1 cm. long, 5 mm. thick; seeds ovoid, 4 mm. long, the testa yellow, minutely verruculose.

On trees in humid forest, or sometimes in rather exposed and dry places, generally distributed in Central America, and ranging from Colombia to Tobago and Venezuela, at or near sea level.

CANAL ZONE: Barro Colorado Island, *Bailey 72*; Fort Randolph, *Standley 28723*; Río Indio de Gatún, *Pittier 2801*. PANAMÁ: Alhajuela, *Pittier 2344*. BOCAS DEL TORO: Bocas del Toro, *Carleton 377*; Shepherd Island, Chiriquí Lagoon, *Wedel 2721*.

This is an abundant plant in many parts of the Panama lowlands as well as generally along the Atlantic coast of Central America. The plants often attain a huge size, and have a great number of densely clustered leaves, below which hang, on pendent peduncles, the heavy fruiting spadices whose bright coloring is certain to attract attention. Illustrated, *Pflanzenreich IV. 23B: fig. 24*.

18. *ANTHURIUM MAXIMUM* (Desf.) Engler, *Pflanzenreich IV. 23B:77. 1905*.
Pothos maxima Desf. Cat. 8. 1829.

Plants epiphytic, very large and coarse, acaulescent or nearly so, with a dense cluster of large leaves; petioles much shorter than the blades (in specimens seen about 16 cm. long), 5-carinate dorsally, with a short and very thick node, 1.5–2 cm. thick; blades coriaceous when dried, obovate or obovate-oblong, about 50 cm. wide, cuspidate, gradually cuneate-attenuate to the narrow base, the costa very thick and salient, carinate, the primary lateral nerves 14–16 on each side, thick, remote, very prominent, not united to form a distinct collective nerve; peduncles about 60 cm. long, 5- to 7-angulate, very stout, terete near the apex; spathe linear-lanceolate, short-decurrent at the base, about 45 cm. long and 2 cm. wide; spadix sessile, caudiform, 50–60 cm. long, dull green; berries bright red, pyriform, 1 cm. long, 4–5 mm. thick at the apex; seeds oblong, somewhat compressed, 5 mm. long, the testa yellow, very minutely verruculose.

On trees in humid forest, Panama and Colombia; in Colombia occurring at 1,400 meters.

CANAL ZONE: Frijoles, *Pittier 2679*.

The single Panama collection was determined by Krause. The leaves are larger than those of any other Panama species having entire leaf blades.

19. *ANTHURIUM PITTIERI* Engler, *Bot. Jahrb. 25:373. 1898*.

Plants small, epiphytic, the caudex elongate, sometimes 1 cm. thick but usually much more slender, the internodes mostly elongate; cataphylls deciduous, obtuse, 4–5 cm. long, 5–6 mm. wide; petioles slender, short-vaginate, 5–9 cm. long,

geniculate about 1 cm. below the apex, the node slender; blades coriaceous when dried, thick and succulent in the living state, oblong-lanceolate, 5–12.5 cm. long, 2.5–4 cm. wide, rather abruptly caudate-attenuate, acute at the base, the primary lateral nerves 7–9 on each side, very slender and inconspicuous, erect-patent, united to form an inconspicuous, slender collective nerve near the margin; peduncles slender, twice as long as the petioles or shorter, up to 15 cm. long, the stipitiform portion 1.5–3 cm. long; spathe linear-lanceolate, acuminate, long-decurrent on the peduncle, 7–8 cm. long or shorter, 1 cm. wide, pale green; spadix at anthesis 4–5 cm. long, in fruit 8 cm. long, 3–4 mm. thick, obtuse; sepals 2.5 mm. long, 4 mm. wide, dull purplish; ovary ovoid, 2 mm. long, the stigma subsessile; berries short-ovoid, pale green, 1- or 2-seeded, 3 mm. long and thick; seeds oblong, 1.5 mm. long.

On trees in humid forest, Panama and Costa Rica, at 600 to 3,000 meters.

CHIRIQUÍ: Los Sigüas Camp, southern slope of Cerro de la Horqueta, 1700 m., *Pittier* 5736. DARIÉN: Cana-Cuasi trail, 600 m., M. E. & R. A. *Terry* 1442.

Illustrated, *Pflanzenreich* IV. 23B: fig. 26. The leaves usually are fuscous when dried.

20. *ANTHURIUM TRINERVE* Miq. *Linnaea* 17:67. 1843.

Anthurium trinerve Miq. var. *obtusum* Engler, *Bot. Jahrb.* 25:357. 1898.



Fig. 78. *Anthurium trinerve*

Amazonian Brazil.

Plants epiphytic, the caudices elongate, emitting many long roots, covered by the fibrous remains of the cataphylls, the internodes short or elongate; petioles slender, one-third to two-thirds as long as the blade, semiterete, geniculate; blades subcoriaceous when dried, lanceolate or oblong-lanceolate, 5.5–11.5 cm. long, 1.5–4.5 cm. wide, long-acuminate to acute, acute at the base, densely punctate beneath, the primary lateral nerves very slender and inconspicuous, united to form a distinct collective nerve remote from the margin; peduncles very slender, 2–3 times as long as the petioles; spathe ovate-lanceolate, 1–1.5 cm. long, or sometimes 2.5 cm. long and 1 cm. wide, pale yellowish green, acuminate; spadix cylindric, obtuse, about 2 cm. long or in fruit 2.5–3.5 cm., bluish green or purple at first; berries white.

Humid forest, on trees or sometimes on rocks, Costa Rica to British Guiana and

BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoö, 10–50 m., Woodson, Allen & Seibert 1880; Old Bank Island, Chiriquí Lagoon, Wedel 2046, 2171; Chiriquí Lagoon, Wedel 1149. CHIRIQUÍ: Cerro de Lino, above El Boquete, 1300–1560 m., Pittier 3028; Bajo Chorro, Boquete District, 1800 m., Davidson 162; vicinity of Bajo Mona and Quebrada Chiquero, 1500 m., Woodson & Schery 570.

It seems probable that this should be reduced to synonymy under *A. scandens*, or at most constitute a variety of that species. Peduncle length alone hardly can be considered a character of specific importance, when one considers the amount of individual variation found in other species of the genus.

21. *ANTHURIUM SCANDENS* (Aubl.) Engler in Mart. Fl. Bras. 3²:78. 1878.

Dracontium scandens Aubl. Pl. Guian. 2:836. 1775.

Anthurium rigidulum Schott, Oesterr. Bot. Zeitschr. 8:180. 1858.



Fig. 79. *Anthurium scandens*

Plants epiphytic, the caudices elongate, often branched, becoming suffrutescent, rather stiff, usually emitting many long roots from the nodes, the internodes short or elongate, usually covered by fibrous remains of the cataphylls; petioles slender or rather stout, one-fifth to one-half as long as the blades, dilated at the base, geniculate near the apex and slightly dilated; blades subcoriaceous when dried, densely punctate beneath, lanceolate to oblong-lanceolate or sometimes lance-ovate, mostly 4.5–9 cm. long and 2–4 cm. wide, acuminate to subobtuse, acute at the base or rarely obtuse or rounded, the primary lateral nerves numerous, very slender, prominent beneath but not conspicuous, united to form a distinct but slender collective nerve near the margin; peduncles slender, equaling or slightly exceeding the petioles; spathe green or pale green, lanceolate or oblong-lanceolate, usually 2.5 cm. long or less, cuspidate,

reflexed; spadix sessile or nearly so, in anthesis about 2 cm. long, very obtuse, in fruit often 4.5 cm. long; berries globose, usually lavender or pale purple, sometimes white, about 5 mm. in diameter.

On trees or rocks in humid forest, rarely in exposed and rather dry situations, southern Mexico to the Guianas and southern Brazil, ranging from sea-level up to 2,100 meters or more.

CANAL ZONE: Bohío, Pittier 3424; Barro Colorado Island, Shattuck 1028; Kenoyer 194; lake shore along Gatún River valley, Pittier 6515. BOCAS DEL TORO: Western River, Wedel 20; Water Valley, Chiriquí Lagoon, Wedel 1558; Isla Colón, Chiriquí Lagoon, Wedel 1290; Fish Creek, Chiriquí Lagoon, Wedel 2390; Nievecita, Woodson, Allen & Seibert 1873. CHIRIQUÍ: between Alto de las Palmas and top of Cerro de la Horqueta, 2100 m., Pittier 3259; Casita Alta, Volcán de Chiriquí, 1500–2000 m., Woodson, Allen

♂ Seibert 925; Volcán de Chiriquí, 2100 m., Davidson 913; Boquete, Davidson 734. COCLÉ: north rim, El Valle, Allen 1812.

Although a relatively small and inconspicuous plant as compared with most epiphytic Araceae, this is perhaps the most abundant and widely distributed member of the family in Central America. It is easy of recognition because of its small, 3-nerved leaves, pointed at each end. The usually lavender berries are rather handsome. Illustrated, Pflanzenreich IV. 23B: fig. 21; HBK. Nov. Gen. & Sp. 1: pl. 19; Hook. Exot. Fl. pl. 55; Lodd. Bot. Cab. pl. 632; Saunders, Refug. Bot. pl. 257.

22. *ANTHURIUM MYOSUROIDES* (HBK.) Endl. Gen. 240. 1837.

Pothos myosuroides HBK. Nov. Gen. & Sp. 1:62, pl. 18. 1815.

Anthurium myosuroides (HBK.) Endl. var. *angustifolium* Engler, Bot. Jahrb. 25:382. 1898.

Plants epiphytic, the caudices elongate and creeping or scandent, less than 3 mm. in diameter, green, rooting at the nodes, the internodes mostly elongate; cataphylls short, linear-attenuate, caducous; petioles slender, sometimes almost equaling the blades but usually much shorter, 15 cm. long or less, geniculate 1–2.5 cm. below the apex, the node slender; blades membranaceous and usually bright green when dried, slightly paler beneath, epunctate, ovate-elliptic to ovate-oblong or oblanceolate-oblong, mostly 13–20 cm. long and 4–9 cm. wide, cuspidate-acuminate to attenuate, somewhat narrowed to the obtuse or narrowly rounded and shallowly cordate base, the basal lobes small and broadly rounded, separated by an open sinus, quintuplinerved at the base, the upper 2 nerves arising far above the base, the primary lateral nerves 9–10 on each side, very slender, united to form a slender collective nerve remote from the margin; peduncles very slender, 7–14 cm. long; spathe lanceolate, acuminate or long-attenuate, 5–7 cm. long, 14 mm. wide or less, pale green; spadix borne on a stipe 5–10 mm. long, or sometimes almost sessile, slender and attenuate upward, 5–8 cm. long or in fruit as much as 12 cm., 3–4 mm. thick in anthesis; berries ovoid, 8 mm. long, orange or scarlet.

On trees in humid forest, Guatemala to Colombia, in Central America usually at low elevations, in Colombia ascending to 2,000 meters; probably also in southern Mexico.

CANAL ZONE: Barro Colorado Island, L. H. & E. Z. Bailey 517, 625; Starry 60. COCLÉ: El Valle, 600–1000 m., Allen 1186. DARIÉN: between Pinogana and Yavisa, Allen 290; Boca de Pauarandó, Sambú River, Pittier 5574.

Pittier 5574 was determined by Krause as *A. mexicanum* Engler (this name is invalidated by *A. mexicanum* Liebm., 1849–50), which may be synonymous with *A. myosuroides*. Var. *angustifolium*, described from Matina, Costa Rica, has leaf blades only 3 cm. wide.

23. *ANTHURIUM GRACILENS* Standl. Field Mus. Bot. Ser. 22:68. 1940.

Plants epiphytic or sometimes terrestrial, the caudex elongate, slender, 4 mm. in diameter, brownish, with elongate internodes; cataphylls linear-attenuate,

brown, deciduous; petioles very slender, slightly shorter than the blades, 10–22 cm. long, geniculate 1–1.5 cm. below the apex, the node slender; blades membranaceous and usually bright green when dried, only slightly paler beneath, epunctate, ovate-elliptic to ovate-oblong, 17–21 cm. long, 6.5–8 cm. wide, cuspidate-acuminate, scarcely at all narrowed toward the base, this broadly rounded and emarginate or subcordate, rarely truncate, 5-nerved at the base, the primary lateral nerves about 9 on each side, ascending at an angle of 45 degrees or usually more, very slender, united near the margin to form a slender, almost regular collective nerve; peduncles about 11 cm. long, very slender; spathe lance-oblong, green, 1 cm. wide or more; spadix borne on a slender stipe 1 cm. long, cylindric, very obtuse, about 4.5 cm. long and 5–6 mm. in diameter.

Mountains of Chiriquí, Panama, at 1300–2000 m., on trees in humid forest.

CHIRIQUÍ: Río Chiriquí Viejo Valley, *Peggy White 160* (TYPE); Bajo Mona, Río Caldera, *Woodson, Allen & Seibert 1026*; Cerro Punta, *Allen 1531*; Río Chiriquí Viejo, 1300–1900 m., *Seibert 146, 219*.

24. *ANTHURIUM MICROSPADIX* Schott, Oesterr. Bot. Zeitschr. 8:180. 1858.

Anthurium tapinostachyum Schott, Oesterr. Bot. Zeitschr. 8:180. 1858.

Plants terrestrial and probably also epiphytic, the caudex creeping or scandent, slender, with short or elongate internodes; cataphylls linear, acuminate, finally deciduous; petioles less than half as long as the blades, 9–18 cm. long, slender, geniculate 1 cm. or less below the apex; blades epunctate, thin when dried, oblong-lanceolate, 20–25 cm. long, 5–7 cm. wide, acute or acuminate, slightly paler beneath, obtuse or rounded at the base, the primary lateral nerves 15–18 on each side, ascending at an angle of about 45 degrees, united to form a distinct, prominent collective nerve near the margin; peduncles longer or shorter than the petioles; spathe lanceolate, acuminate, green, about 4 cm. long; spadix borne on a stipe 4–5 mm. long, obtuse or acute, cylindric, 4–5 cm. long, 3–4 mm. thick.

Humid forest, Costa Rica to Ecuador, chiefly at 250–1,300 meters.

CHIRIQUÍ: Río Ladrillo, above El Boquete, 1200–1300 m., *Pittier 3063*.

The single Panama collection was determined by Krause.

25. *ANTHURIUM PALLENS* Schott, Oesterr. Bot. Zeitschr. 8:180. 1858.

Plants epiphytic, more or less scandent or creeping, with numerous long roots arising from the nodes, the caudex slender, as much as 7 mm. in diameter; cataphylls linear, elongate, brownish, soon deciduous; petioles very slender, sometimes longer than the blades but usually shorter, 12–30 cm. long, geniculate 1–1.5 cm. below the apex, the node very slender; blades almost membranaceous when dried, epunctate, lance-oblong, 12–24 cm. long, 3–6.5 cm. wide, caudate-acuminate, obtuse or rounded at the base, the numerous primary lateral nerves diverging at a rather wide angle, very slender, prominent, united to form a distinct and almost regular collective nerve 3 mm. or more from the margin; peduncles slender, equaling or shorter than the petioles, 20 cm. long or less, very slender; spathe lance-linear, long-acuminate, green or yellowish green, 4–4.5 cm. long,

4–7 mm. wide; spadix conspicuously stipitate, cylindric, 2.5–3.5 cm. long, obtuse, pale yellow or yellowish green; ovary short-ovoid, with a very short style.

Humid forests of the mountains of Costa Rica and Panama, at 1,400–2,600 meters.

CHIRIQUÍ: Bajo Chorro, Boquete District, *Davidson 41*; Upper Río Caldera above El Boquete, *Maxon 5707*; Los Sigüas Camp, Cerro de la Horqueta, *Pittier 3187*; Holcomb's Trail, above El Boquete, *Killip 3521*; vicinity of Bajo Mona and Quebrada Chiquero, 1500 m., *Woodson & Schery 549*.

26. *ANTHURIUM TALAMANCAE* Engler, Bot. Jahrb. 25:387. 1898.

Caudex with short internodes; cataphylls greatly elongate; petioles almost equaling or shorter than the blades, very slender, about 30 cm. long, geniculate 1.5 cm. below the apex; blades subcoriaceous, oblong, about 35 cm. long and 15 cm. wide, caudate-acuminate, subtruncate or subcordate at the base, with very short, rounded basal lobes, the primary lateral nerves 1.5–2 cm. apart, slender but prominent beneath, united 3–4 mm. from the margin to form a distinct collective nerve; peduncles 30 cm. long; spathe linear-lanceolate, long-cuspidate, decurrent at the base, 8 cm. long, 1.5 cm. wide; spadix borne on a stipe 5 mm. long, slender-cylindric, 8–9 cm. long, 5 mm. thick; sepals 1 mm. wide and slightly longer; ovary ovoid.

Known certainly only from the original Panama collection.

BOCAS DEL TORO: Shirores, Talamanca, in forest at 100 m., *Tonduz 9229, 9233* (TYPES). COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2204* (sterile and determination questionable).

27. *ANTHURIUM SCOLOPENDRINUM* (Ham.) Kunth, Enum. Pl. 3:68. 1841.

Pothos scolopendrinus Ham. Prodr. 16. 1825.

Anthurium inconditum Schott, Oesterr. Bot. Zeitschr. 8:181. 1858.

Plants small, epiphytic, the caudex very short or almost none, thick, with short internodes; petioles slender, half as long as the blades or usually much shorter, somewhat dilated at the base, geniculate just below the apex; blades thin and almost membranaceous when dried, oblanceolate or narrowly oblong-oblanceolate, commonly 11–28 cm. long and 2–5 cm. wide, gradually acuminate or long-acuminate, long-attenuate to the very narrow, stipe-like base, the costa slender or stout, prominent, the lateral nerves very numerous, oblique, ascending at an angle of about 45 degrees, slender, united rather remote from the margin to form a distinct collective nerve; peduncles slender, equaling or longer than the leaves, or sometimes shorter; spathe narrowly lanceolate, pale green, usually 2.5 cm. long or less, subulate-attenuate; spadix very slender, sessile or subsessile, green, sometimes 10 cm. long but usually much shorter, obtuse; berries scarlet, 7 mm. long or less, few and scattered in the fruiting spadix.

On trees in humid forest, Guatemala to southern Brazil, chiefly at low elevations but in Costa Rica ascending to 1,200 meters or higher.

CANAL ZONE: Barro Colorado Island, *Kenoyer 187*; L. H. & E. Z. Bailey 406; *Woodworth & Vestal 702*; Caño Quebrado, *Pittier 6657*; without locality, Mrs. Gaillard in 1909; Colón to Empire, *Crawford 557*. PANAMÁ: Río Tapia, *Standley 26218*. DARIÉN: Crest, Cana-Cuasi trail, Chepigana District, M. E. & R. A. Terry 1570. BOCAS DEL TORO: Little Bocas, Chiriquí Lagoon, *Wedel 2532*.

28. *ANTHURIUM MICHELII* Guillaumin, Bull. Mus. Hist. Nat. Paris 31:263. 1925.

Caudex short; petioles one-fifth to one-third as long as the blade, 2.5–6.5 cm. long, geniculate 1 cm. below the apex; blades oblanceolate, 13–21 cm. long, 5–6.5 cm. wide, thick but not coriaceous, membranaceous when dried, attenuate from the upper third to the apex and abruptly acuminate, cuneate-attenuate to the base, the lateral nerves straight, united to form a collective nerve 6–8 mm. from the margin; peduncles 21 cm. long, about equaling the leaves, slender; spathe lanceolate, acuminate, green, 3 cm. long, 8 mm. wide; spadix yellow, borne on a stipe 1 cm. long, green, cylindric, 2.5 cm. long, 4 mm. thick, in fruit as much as 9–15 cm. long; berries ovoid, reddish black, 12 mm. long, 7 mm. thick, slightly attenuate at the apex, dark red above, whitish below, the cells 1-seeded; seeds oblong, 7 mm. long, attenuate at the base, the testa smooth, white.

Known only from Panama. Described from living plants collected by Michel in Panama, the locality unknown.

BOCAS DEL TORO: hills behind Fish Creek, Chiriquí Lagoon, Wedel 2276, 2371.

29. *ANTHURIUM RAMONENSE* Engler ex Krause, Notizbl. Bot. Gart. Berlin 11:611. 1932.

Plants coarse, epiphytic, sometimes terrestrial, the caudex very short or almost none, thick; petioles stout, 10–16 cm. long, the node short and rather stout; blades subcoriaceous when dried, black-punctate beneath, often densely so, oblanceolate-oblong, 25–38 cm. long, mostly 9–11 cm. wide, rather abruptly short-acuminate, long-attenuate from the upper third to the narrow base, the primary lateral nerves numerous, rather stout and prominent, ascending at an angle of 45 degrees or more, united to form a distinct, regular collective nerve 2–3 mm. from the margin; peduncles slender, terete, 11–35 cm. long; spathe linear-lanceolate, green tinged with dark red, or purplish white, acuminate, 5–10 cm. long, 5–10 mm. wide; spadix sessile, caudiform, 11–22 cm. long, 4–5 mm. thick, reddish brown; sepals oblong; pistils ovoid.

On trees in humid forest, Costa Rica and Panama, ascending from sea-level to 1,200 meters.

CANAL ZONE: Río Indio de Gatún, Pittier 2796; Barro Colorado Island, Standley 41149. BOCAS DEL TORO: Western River, Chiriquí Lagoon, Wedel 2789.

30. *ANTHURIUM HACUMENSE* Engler, Bot. Jahrb. 25:363. 1898.

Anthurium concolor Krause, Notizbl. Bot. Gart. Berlin 11:606. 1932.

Plants epiphytic, rather large and coarse, the caudex short or almost none, very thick; petioles about one-fifth as long as the blades or shorter, stout, short-vaginate, about 10 cm. long, often 1 cm. or more in diameter, the very thick node as much as 2 cm. long; blades coriaceous, oblanceolate-spatulate to obovate-cuneate, commonly 60–70 cm. long and 15–20 cm. wide, obtuse to rounded at the apex and cuspidate-apiculate, gradually narrowed from the upper third to the long, attenuate base, the lateral nerves numerous, the primary ones rather stout and prominent, ascending at an angle of 45 degrees or more, 2.5–3 cm. apart, united to form a distinct, prominent, regular connective nerve 1.5–2 cm.

from the margin; peduncles as much as 50 cm. long, rather stout; spathe 9 cm. long or more, apparently early deciduous; spadix borne on a stout stipe 8–14 cm. long, the spadix cylindric, 12–17 cm. long, 1.5–2 cm. thick, obtuse; sepals 3 mm. long, 1 mm. wide; ovary ovoid, 3 mm. long, contracted into a style 1 mm. long.

On trees in humid forest, Panama and Costa Rica, at 250 meters or less.

CANAL ZONE: Río Indio de Gatún, Pittier 2793, 2797, 2798 (TYPE of *A. concolor*); Frijoles, Pittier 3748; hills north of Frijoles, Standley 27544. COLÓN: Porto Bello, Maxon 5732.

The species is noteworthy for the greatly elongate stipe of the spadix, a character not found in any other Panama species of *Anthurium*.

31. *ANTHURIUM GRACILE* (Rudge) Lindl. Bot. Reg. 19:1635. 1833, excluding plate.

Pothos gracilis Rudge, Pl. Guian. 1:23, pl. 32. 1805.

Anthurium Friedrichsthali Schott, Oesterr. Bot. Wochenbl. 5:65. 1855.

Anthurium gracile (Rudge) Lindl. var. *Friedrichsthali* (Schott) Engler in DC. Monogr. Phan. 2:118. 1879.

Anthurium Rudgeanum Schott, Prodr. Aroid. 448. 1860.

Anthurium linearifolium Engler, Bot. Jahrb. 25:370. 1898.



Fig. 80. *Anthurium gracile*

Plants rather small, epiphytic, the caudex commonly short, thick, with very short internodes, the cataphylls soon weathering into fibers; petioles slender, one-fourth as long as the blades or usually much shorter, subterete, somewhat dilated at the base, nodose near the apex; blades linear or lance-linear, 15–40 cm. long, 1.5–3.5 cm. wide, acute to attenuate-acuminate, cuneately narrowed to the base, very thick and coriaceous when dried, dark green above, slightly paler beneath, punctate on both surfaces, the costa rather stout, very prominent, the primary lateral nerves numerous, ascending at a narrow angle, slender, prominent, at least beneath, united near the margin to form a distinct collective nerve; peduncles slender, equaling or more often shorter than the leaves; spathe reddish, linear or linear-lanceolate, usually 3–4 cm. long and much shorter than the spadix, acute or acuminate; spadix reddish brown, sessile, slender-cylindric, 4–8 cm. long, 3–5 mm. thick, obtuse, slightly attenuate upward; sepals 1.5 mm. wide, 1 mm. long; pistil depressed-globose, about 1.5 mm. wide and 1 mm. long; berries orange-red.

On trees in wet forest, at low elevations, Guatemala to the Guianas, Amazonian Brazil, and Peru.

CANAL ZONE: Balboa, cultivated, *Standley 28556*; hills north of Frijoles, *Standley 27457*; Mohinga Swamp, *Bailey 589*; Gatún, *Hayes*; Barro Colorado Island, *Shattuck 102, 200, 594*; *Aviles 62, 917*; *Standley 31339*; *Kenoyer 186*. COLÓN: Río Fató, *Pittier 3916*. DARIÉN: Pinogana, *Pittier 6525*; Boca de Pauarandó, Sambú River, *Pittier 5682*. COCLÉ: Bismarck, above Penonomé, *Williams 600*. BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *Wedel 1373*.

The material referred here is quite uniform in leaf form, but not too sharply separated from some of the following species. *Pittier 3916*, which differs in no respect from the other collections cited, was determined by Krause as *A. Bakeri* Hook. f., evidently in error. The type of *A. Friedrichsthalii* was collected on Cativo Island by Friedrichsthal, a locality referred by Schott and Engler erroneously to Guatemala. The type of *A. linearifolium* is *Lehmann 4538* from the Río "Chagues" (presumably Chagres), Isthmus of Panama.

32. *ANTHURIUM LITTORALE* Engler, Bot. Jahrb. 25:405. 1898.



Fig. 81. *Anthurium littorale*

Plants coarse, epiphytic, the caudex short or almost none, with very short internodes; cataphylls rusty brown, soon weathering into coarse fibers; petioles stout, semiterete, 2.5–5 cm. long, broadly canaliculate, geniculate just below the apex; blades thick-coriaceous when dried, oblong-lanceolate to oblong-elliptic, 14–30 cm. long, 4.5–10 cm. wide, obtuse and apiculate at the apex or subacute and short-cuspidate, acute at the base, the costa very thick and prominent beneath, the primary lateral nerves 9 or more on each side, ascending at a narrow angle, slender, united rather remote from the margin to form a distinct collective nerve; peduncles reported to attain a length of 25 cm. but usually much shorter; spathe linear-lanceolate, one-third as long as the spadix or often much shorter, 5–8 cm. long, 5–10 mm. wide, acute or subobtuse and apiculate; spadix caudiform, obtuse, slightly attenuate upward, often 20 cm. long but in early anthesis frequently much shorter, to 8 mm. in diameter; sepals 2 mm. wide and 1.5 mm. long; ovary depressed-globose.

On trees in humid forest, chiefly at or near sea level, Panama and Costa Rica.

CANAL ZONE: Barro Colorado Island, *Woodworth & Vestal 680; Shattuck 661; Kenoyer 182; L. H. & E. Z. Bailey 400.* COCLÉ: north rim of El Valle, *Allen & Alston 1843a.*

33. *ANTHURIUM ACUTANGULUM* Engler, Bot. Jahrb. 25:371. 1898.

Plants large and coarse, epiphytic, the caudex short and thick, with very short internodes, the cataphylls weathering into coarse, brown fibers; petioles stout, mostly 12–18 cm. long and 5–6 mm. thick, carinate, broadly canaliculate above, geniculate 5–6 mm. below the apex, the node thick, compressed; blades subcoriaceous when dried, elliptic or oblong-elliptic, 20–35 cm. long, 10–13 cm. wide, rounded or obtuse at the apex and cuspidate-acuminate, obtuse at the base or cuneately acute, rarely abruptly contracted, the costa very prominent beneath, rather stout, the primary lateral nerves about 9 on each side, distant, ascending at a rather wide angle, united remote from the margin to form a distinct collective nerve; peduncles slender or stout, often equaling the leaves but frequently much shorter; spathe attaining at least 7 cm. in length (no perfect one seen), often deciduous; spadix caudiform, very slender, sessile or short-stipitate, 15–23 cm. long, 4–6 mm. thick, very slightly attenuate upward, obtuse; sepals 3 mm. wide, 2 mm. long; ovary subglobose, 2 mm. in diameter; berries 5 mm. in diameter.

On trees in humid forest, usually at or near sea-level but ascending to 1,650 meters, Panama and Costa Rica.

CANAL ZONE: Río Indio de Gatún, *Maxon 4865; Pittier 2796, 2799;* Barro Colorado Island, *Aviles 16.* COLÓN: Río Sirrí, *Pittier 4024.* DARIÉN: Crest, Cana-Cuasi trail, Real District, 1650 m., *M. E. & R. A. Terry 1580.*

34. *ANTHURIUM JOSEANUM* Engler, Pflanzenreich IV. 23B:68. 1905.

Anthurium validifolium Krause, Notizbl. Bot. Gart. Berlin 11:607. 1932.

Plants rather coarse and stout, epiphytic, the caudex short and thick, often almost none, the long cataphylls soon weathering into abundant, coarse fibers; petioles rather stout, half as long as the blades or often much shorter, rounded dorsally, geniculate near the apex; blades coriaceous when dried and usually pale, elongate-lanceolate or merely lanceolate, 30–70 cm. long and 4–9 cm. wide or even larger, gradually long-attenuate, narrowed toward the acute base, about equally narrowed to each end, the costa slender or rather stout, very prominent beneath, the primary lateral nerves often as many as 20 on each side, ascending usually at an acute angle but sometimes spreading rather widely, slender but strongly salient, united near the margin to form a distinct collective nerve; peduncles slender, equaling or often much longer than the petioles; spathe lanceolate, sometimes 15 cm. long and 2 cm. wide at the base but often much smaller, purplish or yellowish green; spadix caudiform or slender-cylindric, short-stipitate or almost sessile, reddish purple, attenuate upward and obtuse, in fruit as much as 25 cm. long and 8 cm. thick, at anthesis usually smaller; sepals 3.5 mm. long; pistils oblong, 5–6 mm. long; berries orange.

On trees or rarely terrestrial, mostly at middle or rather high elevations, Panama and Costa Rica.

BOCAS DEL TORO: Río Cricamola, 10–50 m., *Woodson, Allen & Seibert 1889* (perhaps a distinct species); Isla Colón, *Wedel 125*. CHIRIQUÍ: Río Ladrillo above El Boquete, 1200 m., *Pittier 3052* (TYPE of *A. validifolium*), 3160, 3161, 3062; Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 970*; Chiriquí Viejo, 1300–1900 m., *Seibert 172*, 289; Bajo Chorro, Boquete District, 1800 m., *Davidson 225*, 276; Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m., *Allen 1506*; Quebrada Velo, 1800 m., *Woodson & Schery 253*, 265.

The material referred here is slightly variable and it is possible that more than a single species is represented. At first glance one would take *A. validifolium* to be a distinct species, but closer examination has failed to reveal any dependable character by which it may be separated.

35. *ANTHURIUM TURRIALBENSE* Engler, Bot. Jahrb. 25:406. 1898.

Plants epiphytic, the caudex short and thick, with very short internodes, the cataphylls soon weathering into brown fibers; petioles rather stout and angulate, one-fourth as long as the blades, geniculate 7 mm. below the apex, the node thick; blades coriaceous when dried, conspicuously black-punctate on both surfaces, linear-lanceolate, 40–65 cm. long, 4.5–6 cm. wide, attenuate-acuminate, gradually cuneate-attenuate to the base, the primary lateral nerves very numerous, slender, prominent, scarcely stouter than the secondary ones, ascending at an angle of about 45 degrees, united 5 mm. from the margin to form a distinct collective nerve; peduncles twice as long as the petioles, rather slender; spathe broadly linear, 3–6.5 cm. long, 1 cm. wide or less, apiculate; spadix short-stipitate, 6–12.5 cm. long, 5–7 mm. thick, obtuse, slightly attenuate upward.

On trees in humid forest, at 500 m. or less, Panama and Costa Rica.

CANAL ZONE: Barro Colorado Island, *Standley 31386*, 40887; *Bailey 626*. SAN BLAS: hills of Sperdi, near Puerto Obaldía, *Pittier 4414*. BOCAS DEL TORO: Isla Colón, Chiriquí Lagoon, *Wedel 2857*.

The Barro Colorado specimens are sterile and it is quite possible that they represent a distinct species, since their leaves are proportionately broader than in the typical form.

36. *ANTHURIUM CHIRIQUENSE* Standl. Field Mus. Bot. Ser. 22:67. 1940.

Plants rather large and coarse, epiphytic, the caudex short and thick, with very short internodes, the numerous cataphylls weathering into coarse, stramineous fibers; petioles subterete, almost equaling the blades, 20–30 cm. long, stout, geniculate about 8 mm. below the apex, the node thick; blades narrowly elliptic-oblong, mostly 29–35 cm. long and 7–10 cm. wide, obtuse at the apex and abruptly cuspidate-acuminate, broadly cuneate or subobtuse at the base, subcoriaceous when dried, epunctate, the costa slender, prominent on both surfaces, the primary lateral nerves numerous, not or scarcely stouter than the secondary ones, ascending at an angle of about 45 degrees, united 5–9 mm. from the margin to form a distinct collective nerve; peduncles stout, 45 cm. long, usually almost twice as long as the petioles; spathe purplish green, oblong-lanceolate, 6.5 cm. long, 1 cm. wide, acuminate; spadix purplish, slender-cylindric, obtuse, sometimes slightly attenuate upward, 12–25 cm. long, 7 mm. thick near the base.

Known only from western Panama, at 1000–1800 m., growing on trees in rain forest.

CHIRIQUÍ: Bajo Chorro, Boquete District, *Davidson 283* (TYPE), 312. COCLÉ: hills north of El Valle de Antón, *Allen 2165*.

37. *ANTHURIUM ALLENII* Standl. Field Mus. Bot. Ser. 22:66. 1940.

Plants epiphytic, the caudex short and thick, with very short internodes, the cataphylls weathering into coarse, brown fibers; petioles rather slender, 20–26 cm. long, geniculate 10–14 mm. below the apex, the node no thicker than the petiole; blades oblong-lanceolate, slightly widest toward the base, subcoriaceous when dried, dark-punctate on both surfaces, 30–40 cm. long, 6.5–10.5 cm. wide, acuminate and abruptly cuspidate, obtuse or short-cuneate at the base, the slender costa prominent on both surfaces, the primary lateral nerves numerous, very slender, only slightly prominent, scarcely or not at all stouter than the secondary ones, ascending at an angle of about 45 degrees, united 7 mm. from the margin to form a distinct but very slender collective nerve; peduncles 18–35 cm. long, slender, longer or shorter than the petioles; spathe oblong-lanceolate, 5 cm. long, 1 cm. wide, apiculate; spadix short-stipitate, cylindric or almost caudiform, in anthesis narrowed upward and about 9 cm. long, 5 mm. thick, in age 14 cm. long and almost 1 cm. thick.

Known only from the type region, Province of Coclé, Panama, at 100–800 meters, growing on trees in wet forest.

COCLÉ: north rim of El Valle, *Allen & Alston 1819* (TYPE), 1854.

3. *UROSPATHA* Schott

UROSPATHA Schott, Aroid. 3. 1853.

Terrestrial plants, growing in swamps, the rhizome horizontal or vertical, spongy; leaves basal, few, the petioles elongate, vaginate only at the base, smooth or verrucose, the blade sagittate, the primary lateral nerves ascending at a narrow angle, the secondary nerves transverse and reticulate; peduncle terminal, equaling or longer than the leaves; spathe erect, usually colored outside, whitish within, convolute below, open at the middle and above, the limb usually long-attenuate, contorted, and persistent; spadix short-stipitate or sessile, much shorter than the spathe, densely many-flowered, bearing near the base sterile flowers similar to the fertile ones but smaller; flowers perfect, perigoniate; sepals 4–6, fornicate, subtruncate at the apex; stamens 4–6, the filaments rather broad, compressed, abruptly contracted at the apex into the connective, scarcely longer than the ovary; anthers longer than the connective, the cells ovate-elliptic, dehiscent by an extrorse, apical slit; pistil truncate-conic, incompletely 2-celled, the ovules 2 or more in each cell, attached by long funicles; berry 2-celled, surrounded by the accrescent perianth, by abortion 1- or 2-seeded.

Engler enumerates 15 species, all native in tropical America, three of them described from Central America.

1. *UROSPATHA GRANDIS* Schott, Bonplandia 7:128. 1857.

Leaves unknown; spathe 40–45 cm. long, open from the base upward, scarcely contorted at the apex, at the base as much as 15 cm. wide; spadix rather long-stipitate, 4.5–7 cm. long, 1 cm. in diameter, very obtuse, the stipe adnate dorsally to the spathe.

Known only from the original Panama collection.

CANAL ZONE: Chagres, *Fendler* 434.

Probably synonymous is *Urospatha Tonduzii* Engler, Anal. Inst. Fis.-Geogr. Costa Rica 8:364. 1895, described from Matina on the Atlantic Coast of Costa Rica. This can be decided only when complete material of the Panama plant has been collected. *U. grandis* was described from inflorescences only. A cotype is in the herbarium of the Missouri Botanical Garden. In Central America the species of the genus seem to be confined to *Manicaria* swamps of the Atlantic coast.

4. *MONSTERA* Adans.

MONSTERA Adans. Fam. Pl. 2:470. 1763.

Large and coarse, scandent epiphytes, rooting at the nodes; leaves distichous, the juvenile ones usually appressed to the tree trunk, ovate or ovate-cordate, short-petiolate, not perforated; petioles vaginate to the middle or higher, the sheath persistent or deciduous; blades various, entire and asymmetric or more often perforated or pinnatifid; peduncles terminal, solitary or several; spathe ovate or oblong-ovate, apiculate, cymbiform-convolute, closed after fecundation, finally deciduous; spadix sessile, free, cylindric, densely many-flowered, shorter than the spathe, the lowest flowers sterile, the others perfect, naked; stamens 4, the filaments rather broad and compressed, abruptly narrowed into the slender, acuminate connective, scarcely longer than the pistil; anthers 2-celled, the cells oblong, apiculate, longer than the connective, dehiscent by lateral slits; ovary obconic-prismatic, 2-celled, the cells 2-ovulate; ovules anatropous, on very short funicles; style equaling the ovary but thicker, truncate at the apex and slightly elevated at the middle, the stigma depressed-oblong or linear; fruits crowded, baccate, juicy; seeds obverse-ovate or subcordate, subcompressed.

An American genus, of about 30 species, 11 of which have been recorded as Central American. The plants constitute a large element of the conspicuous epiphytic vegetation of the lowland forests, where they are more than ordinarily conspicuous because of their large and curious leaves, usually either perforated or pinnatifid. Some of the species have become common house and hot-house plants in the United States. Their succulent foliage withstands well the trying effect of steam-heated air. The fully ripened spadices are juicy and sweet, and rather good to eat. The long, flexible, tough aerial roots of *Monstera* and *Philodendron*, which often attain a length of several meters, are much used in some parts of Central America for making the so-called "mimbre" furniture, much like the willow or

rattan furniture of the United States. In Guatemala and Salvador, for instance, this is quite an important industry.

- | | |
|--|-------------------------|
| a. Leaves entire, not perforated..... | 1. <i>M. PITTIERI</i> |
| aa. Leaves pinnatifid or entire and perforated. | |
| b. Leaf blades regularly pinnatifid..... | 2. <i>M. DELICIOSA</i> |
| c. Blades perforated along the costa..... | 3. <i>M. DILACERATA</i> |
| cc. Blades not perforated..... | |
| bb. Leaf blades not regularly pinnatifid, often entire, sometimes cleft to the perforations in a few places..... | 4. <i>M. PERTUSA</i> |



Fig. 82. *Monstera Pittieri*

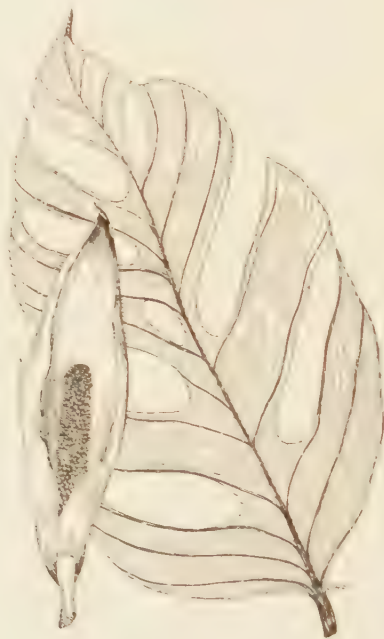


Fig. 83. *Monstera deliciosa*

1. *MONSTERA PITTIERI* Engler, Bot. Jahrb. 37:116. 1905.

A small, epiphytic vine, the caudex slender, its internodes mostly 4–5 cm. long; petioles almost as long as the blades, vaginate to within about 1.5 cm. of the apex, geniculate 1 cm. below the base of the blade; blades subcoriaceous and usually fuscous when dried, obliquely oblong, 10–20 cm. long, 3.5–8.5 cm. wide, short-acuminate, very oblique at the base, the primary lateral nerves slender, few, extending to the margin; peduncles slender, 10 cm. long or less; spathe broadly oblong, 4–5 cm. long, 2 cm. wide; spadix sessile, cylindric, 3–5 cm. long, in fruit almost 2 cm. thick but at anthesis about 8 mm. thick, obtuse; stamens slightly more than half as long as the pistil, spatulate, the anther cells ovoid, divergent; pistil cylindric.

Humid forests of Panama and Costa Rica, usually at low elevations.

CANAL ZONE: Barro Colorado Island, *Aviles 91; Starry 17; Shattuck 6, 27.* COCLÉ: El Valle, 600–1000 m., *Allen 1227.*

2. *MONSTERA DELICIOSA* Liebm. Vid. Medd. Naturh. For. 19. 1850.

A large, coarse, epiphytic vine, often climbing high on trees, the caudex terete, as much as 6 cm. or even more in diameter, the internodes often 7 cm. long or more, the nodes frequently emitting long aerial roots that dangle far below the caudex; petioles 1 m. long or less, 2–2.5 cm. in diameter, the sheath ending far below the base of the blade, the node as much as 3 cm. long; blades of the primary leaves small, cordate, entire, of the succeeding leaves ovate-cordate and sparsely perforated; blades of the adult leaves 40–60 cm. wide or larger, thick-coriaceous when dried, bright green and lustrous above, somewhat paler beneath, cordate-ovate in outline, almost regularly pinnatifid and with few or numerous perforations along the costa, the segments linear or broadly linear, somewhat dilated toward the apex and cuspidate-acuminate; peduncles 10–15 cm. long, 1–1.5 cm. thick; spathe coriaceous, broadly ovate, apiculate, 20–25 cm. long, 15–17 cm. wide when spread out, pale yellowish; spadix 17–20 cm. long, becoming thick and juicy in fruit; pistils turbinate; berries pale yellow, somewhat tinged with violet, 1 cm. long.

On trees in humid lowland forest, Panama to southern Mexico.

CANAL ZONE: Barro Colorado Island, *Kenoyer 183*. CHIRIQUÍ: Río Boquete below Quiel, 1000–1300 m., *Pittier 3151*; Bajo Chorro, 1900 m., *Woodson & Schery 634*.

This species is well known in some parts of Central America, as well as in Mexico, by the name *Piñanona*. It is the species of *Monstera* most often seen in cultivation in the United States and elsewhere. The fruiting spadices are larger than those of other species, sweet and juicy when fully ripened, and rather good to eat.

3. *MONSTERA DILACERATA* C. Koch, Ind. Sem. Hort. Berol. App. 5. 1855.

A large vine, the caudex often greatly elongate, as thick as a finger, the internodes 3–12 cm. long; blades of the juvenile leaves oblong-elliptic, gradually narrowed to the apex, acute or subobtusate at the base; petioles of the adult leaves 25–35 cm. long, stout, marginate almost to the node; blades fuscous when dried and subcoriaceous, obliquely oblong-ovate in outline, commonly rounded or emarginate at the base and abruptly contracted to the petiole, not perforated but almost regularly pinnatifid, with 3–5 divisions on each side, these broadly linear, long-acuminate or attenuate, usually 3–4 cm. wide; peduncles stout, 15–20 cm. long; spathe ovate, yellowish, about 12 cm. long; spadix cylindric, obtuse, 5–6 cm. long, 1.5 cm. thick; pistils prismatic, 4–5 mm. long, the stigma oblong.

On trees in humid lowland forest, sometimes ascending to 1700 m., Costa Rica to Colombia, and probably farther southward.

PANAMÁ: Barro Colorado Island, *Standley 41037*; *Aviles 45*; *Kenoyer 179*; *Frost 206*. CHIRIQUÍ: Callejón Seco, Volcán de Chiriquí, 1700 m., *Woodson & Schery 501*.

The name *Bejuco de Murciélago* is reported locally for the species.

4. *MONSTERA PERTUSA* (L.) de Vriese, Hort. Spaarn-Bergens. 40. 1839.

Dracontium pertusum L. Sp. Pl. 968. 1753.

Monstera Seemannii Schott, Oesterr. Bot. Zeitschr. 9:40. 1859.

Usually a large, epiphytic vine, the caudex terete, 1–3 cm. thick, the internodes 5–10 cm. long; blades of juvenile leaves ovate, oblong-ovate, or oblong-elliptic, entire and not perforated; petioles of adult leaves 20–35 cm. long, vaginate to the node; blades ovate-oblong to almost rounded-ovate, commonly 30–40 cm. long and 15–20 cm. wide, acute and usually cuspidate-acuminate or short-cuspidate, rounded or short-cuneate at the base, with few or numerous large and small perforations, the smaller ones irregularly scattered or absent, some of the perforations usually extending to the margin, the blade thus somewhat pinnatifid although not regularly so; peduncles 10–15 cm. long; spathe coriaceous, oblong, acuminate, 15–20 cm. long, 10 cm. wide when expanded, greenish at first, becoming whitish or yellowish; spadix cylindric, in fruit about 10 cm. long and 1.5–2 cm. thick; pistils subprismatic, 4 mm. long; berries obovoid, pale, 5–6 mm. long, mostly 1-seeded; seeds obliquely cordiform, smooth, brown, 4 mm. long, laterally somewhat compressed.

On trees in humid forest, chiefly at low elevations, southern Mexico to the West Indies and southern Brazil.

CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley* 25736; Ancón, *Pittier* 2752. COLÓN: Fató, *Pittier* 3841. PANAMÁ: Río Tapia, *Standley* 28133; Taboga Island, *Standley* 27877; between Matías Hernández and Juan Díaz, *Standley* 31990; near Arraiján, *Woodson, Allen & Seibert* 1339; savannas north of Panamá, *Bro. Paul* 547. CHIRIQUÍ: southern slope of Cerro de la Horqueta, 1700 m., *Pittier* 3178, 3179; Quebrada Velo, 1800 m., *Woodson & Schery* 279. BOCAS DEL TORO: Johns Creek, Chiriquí Lagoon, *Wedel* 2755; Isla Colón, Chiriquí Lagoon, *Wedel* 2609.

Illustrated, *Pflanzenreich* IV. 23B:104. The material referred here is variable and difficult to understand. Moreover, only a few of the collections are in good condition for study. It is probable that more than a single recognizable form is represented, but more material will be necessary before a satisfactory disposition of the allied local forms can be made. One of the Chiriquí collections was referred by Krause to *M. Parkeriana* Schott, and it does agree perfectly with a photograph of the type of that species. However, it is not apparent how *M. Parkeriana* is to be separated from *M. pertusa*, which Engler calls a "Typus polymorphus." Some of the Canal Zone specimens have been reported as *M. Friedrichsthali* Schott, but apparently in error, that being a Costa Rican plant whose leaves have much more abundant perforations. H. H. Bartlett, who has studied some of the material here cited, has labeled some of the sheets as *M. obliqua* (Miq.) Walp., but in that species, as described by Engler, the spathes are much smaller than in any Panama specimens that I have seen. Bartlett also has labeled some of the sheets from the Zone region as a new species, but the description of any new species in the genus, with the material now available, is scarcely to be recommended. The local name of *Hierba de Puerco* is reported for *M. pertusa*.

5. SPATHIPHYLLUM Schott

SPATHIPHYLLUM Schott, Melet. 1:22. 1832.

Terrestrial, acaulescent herbs, rarely with a short caudex; petioles equitant,

usually long and slender, mostly geniculate near the apex and terete above the node, commonly vaginate to or above the middle; blades mostly oblong to ovate or lanceolate and cuspidate-acuminate, drying rather thin, the costa stout, the primary and secondary lateral nerves subparallel, approximate, ascending chiefly at a narrow angle, not united into a collective nerve; peduncles equaling or longer than the leaves, the spathe cuspidate, decurrent upon the peduncle, membranaceous, convolute in bud, explanate in anthesis, white or whitish; spadix sessile or stipitate, cylindric, erect, shorter than the spathe, densely many-flowered, flowering from the base upward; flowers perfect, perigoniate, typically 3-parted, sometimes 2- to 4-parted; sepals fornicate at the apex and subtruncate, coherent or united to form a truncate cup; stamens as many as the sepals and opposite them, the short filaments dilated and thickened at the apex, gibbous posteriorly, abruptly narrowed at the apex into the connective; anthers ovoid, the cells oblong, exceeding the connective, the cells subopposite, dehiscent by a longitudinal slit that scarcely extends to the base; ovary oblong, commonly 3-celled, the cells 2- to 8-ovulate, the ovules anatropous, attached by short funicles; style continuous with the ovary, conically elongate, and projecting beyond the perianth, or almost none; stigma 3- or 4-lobate, sessile; fruit baccate, rounded or conic at the apex, 3-celled, the cells 1- to 8-seeded; seeds oblong, slightly curved, somewhat reniform, pale yellowish, the testa sparsely striate-verrucose; endosperm abundant.

Engler and Krause recognize 27 species, widely distributed in tropical America, with one species in the Philippines and the central Malayan region. Seven species are known from Central America.

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|--|-------------------------------|
| a. Style very short, not or scarcely exceeding the perianth, the fruiting spadices almost smooth, not tuberculate. | |
| b. Leaves mostly 3-7 cm. wide, the blades acute at the base; spadix 2-6 cm. long. | 1. <i>S. FLORIBUNDUM</i> |
| bb. Leaves mostly 13-20 cm. wide, the blades obtuse or rounded at the base; spadix 9-12 cm. long. | 5. <i>S. FULVOVIRENS</i> |
| aa. Style elongate, conspicuously exceeding the perianth, the fruiting spadices thus strongly tuberculate. | |
| b. Spadix only 1.5 cm. long, few-flowered; leaf blades less than 6 cm. wide. | 2. <i>S. ZETEKIANUM</i> |
| bb. Spadix usually 5-10 cm. long, with very numerous flowers; leaf blades mostly more than 10 cm. wide. | |
| c. Leaf blades acute at the base; cells of the ovary 6- to 8-ovulate. | 3. <i>S. FRIEDRICHSTHALII</i> |
| cc. Leaf blades rounded at the base; cells of the ovary 2-ovulate. | 4. <i>S. PHRYNIIFOLIUM</i> |

1. *SPATHIPHYLLUM FLORIBUNDUM* (Linden & André) N. E. Brown, Gard. Chron. n. s. 10:783. 1878.

Anthurium floribundum Linden & André, Ill. Hort. 21: pl. 159. 1874.

Leaves few or numerous, erect, the petioles 10-21 cm. long, geniculate 5-15 mm. below the apex, conspicuously vaginate, the green sheath extending sometimes almost to the apex of the petiole; blades oblong-lanceolate or oblong-elliptic, 13-24 cm. long, 2.5-7 cm. wide, very narrowly attenuate-acuminate, narrowed to the acute and slightly unequal base, the primary lateral nerves about 20 on each side, ascending at a narrow or rather wide angle; peduncles 20-35 cm. long, very slender, the stipitiform portion 5-10 mm. long; spathe white or green and white,



Fig. 84
Spathiphyllum floribundum

6–10 cm. long, 2–3 cm. wide, narrowly long-cuspidate-attenuate; spadix whitish or greenish yellow, cylindric, slightly attenuate to the apex, 2–6 cm. long, 5–8 mm. thick; sepals 1.5 mm. long and equally wide; pistils short-obpyramidal, 1.2 mm. long, the cells 1- or 2-ovulate.

Dense, wet forest, usually growing on the banks of small streams or on rocks along their banks, Panama to Colombia, at 800 meters or less.

CANAL ZONE: Río Paraíso, above East Paraíso, Standley 29846; reported by L. H. Bailey from Barro Colorado Island, L. H. & E. Z. Bailey 209. PANAMÁ: Río Tapia, Standley 28125; Río Chararé, above Chepo, Pittier 4724. COCLÉ: Río Valle Chiquito, 700–800 m., Seibert 507.

The systematic position of this plant has been clarified recently by Bailey (Gentes Herb. 4:309. 1940). Previously it had been referred (Standley, Fl. Canal Zone 103. 1928) incorrectly to *S. Patinii* (Hogg) N. E. Brown, another Colombian species, distinguished by its much longer petioles, a character perhaps of doubtful systematic importance. Illustrated, Pflanzenreich IV. 23B: fig. 54, A-E; L. H. Bailey, Gentes Herb. 4:308. 1940.

2. *SPATHIPHYLLUM ZETEKIANUM* Standl. in Woodson & Schery, Ann. Missouri Bot. Gard. 27:267. 1940.

Plants slender, about 60 cm. high; leaves numerous, the petioles very slender, 12–20 cm. long, geniculate about 1 cm. below the apex, the sheath short, persistent, scarcely more than 8 cm. long; blades narrowly lanceolate or lanceolate, 13–20 cm. long, 2–5 cm. wide, narrowly long-acuminate, attenuate to the base, deep green above, much paler beneath, the primary lateral nerves about 6 on each side, subremote, ascending at a very acute angle; peduncle terete, slender, about 43 cm. long and 2 mm. thick, the stipitiform portion 3 cm. long; spathe lance-ovate, green, 10.5 cm. long, 3 cm. wide, abruptly caudate-acuminate, acute at the base; spadix cylindric, very obtuse, 1.5 cm. long, 6–7 mm. thick, few-flowered; sepals 6, biseriate, free; style about equaling the ovary, conspicuously exserted beyond the perianth, conic.

Known only from the original collection, from Panama.

CANAL ZONE: Zetek Trail, Barro Colorado Island, D. E. Starry 27 (TYPE).

The foliage is similar to that of *S. floribundum*, but the spadices of the two species, while similar in size, are very unlike in general appearance.

3. *SPATHIPHYLLUM FRIEDRICHSTHALII* Schott, Aroid. 2. *pl.* 4. 1853.*Spathiphyllum Fendleri* Schott, Oesterr. Bot. Wochenbl. 7:9. 1857.*Spathiphyllum lanceolatum* C. Koch, Allgem. Gartenz. 25:174. 1857.Fig. 85. *Spathiphyllum Friedrichsthali*

6- to 8-ovulate.

Wet or damp, usually dense forest, Guatemala to Colombia.

CANAL ZONE: very common, and represented by numerous collections from the Atlantic slope. COCLÉ: north rim of El Valle, *Allen & Alston 1850*. COLÓN: Palenque, near sea level, *Pittier 4122*. BOCAS DEL TORO: Isla Colón, *Wedel 2979*; Río Cricamola, between Finca St. Louis and Konkintoë, *Woodson, Allen & Seibert 1912*; Water Valley, *Wedel 1360*. CHIRIQUÍ: Río Ladrillo, above El Boquete, 1200 m., *Maxon 5390*; El Boquete, 1250 m., *Killip 3639*; Chiquero, 1650 m., *Davidson 565*. DARIÉN: Cana-Cuasi trail, Chepigana District, 1200 m., *M. E. & R. A. Terry 1525*.

The plant is well known in most parts of Central America because of the fact that the young inflorescences are edible. They usually are prepared for the table by frying with eggs, but are treated also in other ways. They seem to be most popular in Salvador and along the Pacific slope of Guatemala. Illustrated, *Pflanzenreich IV. 23B: fig. 49, A-E*. The type of *S. Fendleri* is *Fendler 426* from Chagres.

4. *SPATHIPHYLLUM PHRYNIFOLIUM* Schott, Oesterr. Bot. Wochenbl. 7:159. 1857.

Petioles stout, about 40 cm. long, geniculate 3 cm. below the apex, vaginate

to the middle or higher, the sheath narrow; blades broadly oblong, 35–55 cm. long, 18–23 cm. wide, narrowly long-cuspidate, rounded at the base or abruptly contracted into the petiole, the primary lateral nerves numerous, divergent at an angle of about 70 degrees; peduncles 60 cm. long or more, 5–6 mm. thick, the stipitiform portion 4 cm. long, adnate for three-fourths its length; spathe oblong-elliptic, cuspidate, gradually narrowed at the base and long-decurrent upon the peduncle, 15 cm. long, 5–6 cm. wide; spadix rounded at the apex, 8–10 cm. long, 12–14 mm. thick, or in fruit much thicker; pistils 4–5 mm. long, the style produced far above the perianth.

Moist or wet forest, Guatemala to Panama.

CANAL ZONE: Chagres, *Fendler 425* (TYPE). BOCAS DEL TORO: Shepherd Island, Chiriquí Lagoon, *Wedel 2690*; Old Bank Island, Chiriquí Lagoon, *Wedel 2068*.

The writer strongly suspects that *S. phryniifolium* is a synonym of *S. Friedrichsthalii*, and certainly the differences suggested for separating the two species are not convincing.

5. SPATHIPHYLLUM FULVOVIRENS Schott, Oesterr. Bot. Zeitschr. 8:179. 1858.

Plants almost a meter high; petioles slender, about 60 cm. long, geniculate 2 cm. below the apex; blades broadly elliptic, 30–40 cm. long, 15–20 cm. wide, long-cuspidate, broadly rounded or very obtuse at the base, somewhat asymmetric, the primary lateral nerves 13–15 on each side, divergent at a wide angle; peduncles 70–80 cm. long, 2 cm. or less in diameter, the stipitiform portion 1 cm. long; spathe deep green, oblong-lanceolate, about 12 cm. long and 2.5–3.5 cm. wide, cuspidate; spadix cylindric, 9–12 cm. long, grayish; pistils subturbinate, 4 mm. long, the cells 4-ovulate.

Wet forest, Costa Rica and Panama, the type from Pedregal, Costa Rica.

BOCAS DEL TORO: hills behind Fish Creek, Chiriquí Lagoon, *Wedel 2198*.

6. DRACONTIUM L.

DRACONTIUM L. Sp. Pl. 968. 1753.

Plants terrestrial, usually large, arising from hypogean tubers; leaf one, the petiole very long, vaginate only at the base, often tuberculate and maculate, the blade deeply 3-parted, the segments 2- to 3-parted and again pinnately parted; peduncle short, at least during anthesis; spathe oblong, cuspidate-acuminate, convolute below, open above, persistent; spadix short-stipitate, short-cylindric, free, densely many-flowered, much shorter than the spathe; flowers perfect, perigoniote; sepals 4–8, biseriate, dilated toward the apex and fornicate, irregularly imbricate; stamens 4–6, biseriate, the filaments slightly dilated, subcompressed, abruptly contracted at the apex into the connective; anthers much longer than the connective, linear-elliptic, dehiscent by a vertical slit; ovary ovoid, incompletely 2- to 5-celled, attenuate to the elongate style; ovules solitary; stigmas small, 2- to 5-parted; fruit baccate, surrounded by the perianth, obscurely 2- to 5-lobate; seeds rounded-reniform, somewhat compressed.

About 10 species are known, in tropical America. Three are known from Central America.

1. *DRACONTIUM COSTARICENSE* Engler, Pflanzenreich IV. 23C:44. f. 17. 1911.

Petioles smooth, brown-spotted; blade about 1 meter broad, 3-parted, the central segment pinnately parted, with 3 segments on each side, the ultimate segments cleft to the costa, oblong or oblong-elliptic, as much as 13 cm. long and 5 cm. wide, rounded to obtuse at the apex and often shortly cuspidate-acuminate, the terminal segments often bilobate, thin; peduncles slender, smooth, about 1 m. long, brown-spotted; spathe lanceolate, almost 30 cm. long; spadix short-stipitate, 6.5 cm. long, 1 cm. thick; sepals 6-7, spatulate; stamens becoming slightly longer than the sepals; ovary ovoid, 2-celled; style conoid, longer than the ovary.

Wet lowland forests of Panama and Costa Rica.

CANAL ZONE: Culebra, Pittier 3429.

The Panama record is based upon a single juvenile leaf that is probably referable to this species. The plant evidently is rare in the Zone, since it must be a large and showy one, yet has not been observed by other collectors in the region.

7. *CALADIUM* Vent.

CALADIUM Vent. in Roem. Archiv. 2:347. 1800.

Plants low, acaulescent or nearly so, arising from tuberous rhizomes, with usually only one leaf and one inflorescence arising at the same time from a single tuber; petioles elongate, the blades chiefly sagittate and peltate, the primary nerves few and spreading, the veins densely reticulate; peduncles elongate, solitary; tube of the spathe convolute, persistent, constricted in the throat, the blade cymbiform, white; spadix slightly shorter than the spathe, the lowest part naked and stipitiform, the pistillate inflorescence cylindric-conoid or ellipsoid, densely many-flowered, the sterile staminate portion of the spadix subconic, longer than the pistillate, the fertile staminate portion contiguous with the sterile, subclavate, densely flowered, twice as long as the pistillate part; flowers unisexual, naked; staminate flowers with 3-5 stamens, these connate to form a truncate-obpyramidal synandrium sinuously 6-angulate at the apex, the connective thick, plane at the apex, the anther cells oblong-lanceolate, rounded and emarginate at the base, opening by a short apical slit; ovary 2- or 3-celled, the ovules several in each cell, anatropous, biseriate; style none, the stigma depressed-hemispheric, obscurely 3- or 4-sulcate; fruit baccate, whitish, crowned by the remnants of the stigma, 2- or 3-celled, many-seeded; seeds ovoid, on very short funicles.

Sixteen species are recognized by Engler, all natives of tropical South America.

1. *CALADIUM BICOLOR* (Ait.) Vent. Descr. Cels. pl. 30. 1800.

Arum bicolor Ait. Hort. Kew. 3:316. 1789.

Plant arising from a small, depressed-globose rhizome; petioles very slender, 3 or more times as long as the blade, short-vaginate; blades broadly sagittate-ovate,

mostly 10–20 cm. long, acute or abruptly acute, peltate far above the base, the basal lobes obtuse, directed downward or slightly outward, separated by a broad, open, triangular sinus, the blades thin, glaucescent beneath, spotted above with white, pink, red, pale yellow or other colors; tube of the spathe ovoid, green outside, greenish white within, the blade about twice as long as the tube, cuspidate, white; pistillate portion of the spadix short-cylindroid, yellowish or pale orange, the fertile staminate portion twice as long as the pistillate, cylindric-fusiform.

Original habitat somewhat uncertain, but the plant is probably native of the Amazonian region, perhaps also of the Guianas. Most material in herbaria is taken from cultivated plants or from those naturalized about human settlements.

Panama. Cultivated commonly for ornament, and thoroughly naturalized at some places in the lowlands, particularly in Mount Hope Cemetery, Canal Zone.

Called *Corazón de Jesús* in Panama, and "Wild Coco" by the West Indians resident in the Canal Zone. The plant is well known in cultivation in the North, being highly esteemed for its delicately colored foliage. The leaves exhibit great variation in their coloring, so much so that it is usually difficult to find two plants whose leaves can be said to be exactly or even approximately alike. This species is the so-called "Fancy-leaved Caladium" of the United States. The plant of the same family—but with larger, green leaves—grown there, as well as in tropical America, for ornament under the name "Caladium" or "Elephant-ear" is *Colocasia antiquorum* Schott, native in the Old World tropics.

8. XANTHOSOMA Schott

XANTHOSOMA Schott, Melet. 19. 1832.

Plants usually large and coarse, terrestrial, arising from a hypogean tuber or from a more or less elongate, hypogean or epigeal caudex; petioles long, thick, subterete, vaginate below; blades sagittate, hastate, or trisect or pedatisect, the primary lateral nerves of the blades or their segments united to form a more or less distinct collective nerve; peduncles solitary or aggregate, mostly short; tube of the spathe ovoid or oblong, convolute, persistent, constricted at its apex, the limb oblong-cymbiform or oblong-lanceolate; spadix shorter than the spathe, the pistillate portion cylindric, densely many-flowered, narrowed upward, the sterile staminate part longer than the pistillate, narrowed above, the fertile staminate portion thick-cylindric, slightly narrowed upward, twice as long as the pistillate portion or longer; flowers unisexual, naked; stamens 4–6, connate to form a truncate-obpyramidal, 5- or 6-angulate synandrium truncate at its apex; anther cells obversely oblong-triangular or oblong, opening below the apex of the connective by a short slit; ovaries ovoid, coherent by the thickened, annuliform styles, 2- to 4-celled; ovules several or numerous, anatropous; stigma discoid or hemispheric-discoid, 3- or 4-lobate; berries cylindroid, crowned by the impressed stigma, 3- or 4-celled, the cells many-seeded; seeds ovoid, shorter than the funicles, the testa sulcate.

The genus includes about 40 species, all American. Seven have been reported from Central America.

- | | |
|---|------------------------------|
| a. Leaves pedatisect..... | 1. <i>X. HELLEBORIFOLIUM</i> |
| aa. Leaves entire. | |
| b. Leaves glabrous..... | 2. <i>X. VIOLACEUM</i> |
| bb. Leaves pubescent. | |
| c. Basal lobes of the leaf blade rounded, directed downward, separated by a relatively narrow sinus..... | 3. <i>X. PILOSUM</i> |
| cc. Basal lobes of the leaf blade triangular, directed outward, separated by a very broad and open sinus..... | 4. <i>X. MEXICANUM</i> |

1. *XANTHOSOMA HELLEBORIFOLIUM* (Jacq.) Schott, Oesterr. Bot. Zeitschr. 6:33. 1856.

Arum helleborifolium Jacq. Icon. 3: pl. 613. 1786-93.

Acontias helleborifolius (Jacq.) Schott, Melet. 19. 1832.

Xanthosoma helleborifolium (Jacq.) Schott var. *viride* Engler in Mart. Fl. Bras. 3²:198. 1878.

Caudex tuberous, hypogean; petioles stout and succulent, 20-40 cm. long or more, vaginate for 4-5 cm., glabrous; blades glabrous, thin, green, 20-30 cm. wide and 10-15 cm. long or larger, reniform in outline, pedatisect, the segments 5-13, distant, the lateral ones asymmetric, oblong or lanceolate, acuminate, cuneately narrowed to the base, the central segment oblong, acute, the rachis naked between the segments; peduncles slender, 10-15 cm. long; tube of the



Fig. 86. *Xanthosoma helleborifolium*

spathe green, ovoid, 3-4 cm. long, the blade oblong, cuspidate, 6-10 cm. long, yellowish green; pistillate portion of the spadix 2 cm. long, the fertile staminate about 6 cm., the sterile staminate about 5 cm.; ovaries short-ovoid, whitish.

Wet, lowland forests, Costa Rica to the Lesser Antilles, Guianas, and Amazonian Peru.

CANAL ZONE: Río Pequení, Woodson, Allen & Seibert 1606; Barro Colorado Island, Shattuck 133; Peggy White 148; Bailey 157.

The plant is easy of recognition because of the combination of terrestrial habit and pedately compound leaves. It is reported that a decoction of the foliage of this and other plants is employed locally as one of the numerous remedies for snake bites.

2. *XANTHOSOMA VIOLACEUM* Schott, Oesterr. Bot. Wochenbl. 3:370. 1853.

Rhizome large and tuberous, hypogean; petioles 30–70 cm. long, 1–4 cm. broad at the base, long-vaginate, brownish violaceous; blades at first somewhat pruinose, becoming green, paler beneath, sagittate-ovate, 20–50 cm. long and 15–45 cm. wide or larger, shortly acuminate-apiculate, the basal lobes somewhat triangular, obtuse, separated by an open, acute sinus, the nerves and costa violaceous; peduncles 15–20 cm. long; tube of the spathe as much as 10 cm. long and 4 cm. broad, oblong, glaucous outside, pale yellowish within, the blade oblong-lanceolate, pale yellowish, 15–20 cm. long, 6–7 cm. wide; pistillate portion of the spadix whitish, 4 cm. long, 2 cm. thick, the fertile staminate portion 15 cm. long, the sterile part 4 cm. long; ovaries short-ovoid.

Cultivated commonly in tropical America, Africa, and Asia. Native of tropical America, but the original habitat unknown. Often escaping from cultivation and becoming naturalized, as in Panama.

PANAMÁ: Juan Franco Race Track, Standley 27681; Río Tapia, Standley 28113; Taboga Island, Standley 27875.

Local names are *Otó*, *Badu*, and *Coco*, the last two Jamaican. The plant is cultivated locally for its edible roots which are prepared for the table much like potatoes. Illustrated, Mart. Fl. Bras. 3²:pl. 43.

3. *XANTHOSOMA PILOSUM* C. Koch, Ind. Sem. Hort. Berol. App. 2. 1855.

Plants small and slender, the small, hypogean, tuberous rhizome only about 2.5 cm. in diameter; petioles slender, 15–20 cm. long, densely short-villous; cataphylls numerous and conspicuous, half as long as the petioles or longer, subulate-attenuate, short-villous; blades sagittate-ovate or cordate-ovate, thin,



Fig. 87. *Xanthosoma pilosum*

copiously short-villous or puberulent, especially beneath, 18–30 cm. long, 11–16 cm. wide, cuspidate-acuminate, the basal lobes directed downward, rounded, separated by a narrow, oblong sinus; peduncles slender, 20–25 cm. long, villous; spathe puberulent outside, the tube 4–5 cm. long, the blade ovate-lanceolate or oblong-lanceolate, cuspidate-acuminate, yellowish white, 6–9 cm. long, 2–5 cm. wide; spadix slightly shorter than the spathe, the pistillate portion about 1.5 cm. long, the fertile staminate part 7 cm. long or less, pale yellowish; ovaries short-cylindroid.

Wet, lowland forests, Costa Rica to Colombia; in Colombia reported as ascending to 1,500 meters.

CANAL ZONE: between Gamboa and Cruces, *Pittier* 3774. COCLÉ: in bog, El Valle de Antón, 500–700 m., *Seibert* 491. CHIRIQUÍ: Puerto Armuelles, *Davidson* 1083.

4. *XANTHOSOMA MEXICANUM* Liebm. Vid. Medd. Naturh. For. 15. 1850.

Plants rather small and slender, arising from a small, hypogean caudex; petioles long and slender, puberulent or short-villous; blades deep green and glabrous above, puberulent beneath, broadly sagittate-triangular, 20–30 cm. long, 15–25 cm. wide near the base, cuspidate-acuminate, the basal lobes somewhat triangular, narrowed to an obtuse apex, separated by a very broad and open sinus; peduncles slender, 15–35 cm. long, pilose; tube of the spathe green and purple, 6 cm. long, 2 cm. broad, oblong, pubescent, the limb lanceolate, acuminate, white, pubescent outside, 10–12 cm. long, 4.5–5 cm. wide, cuspidate-acuminate; spadix somewhat shorter than the spathe, the staminate portion slender, about 8 cm. long.

In humid, lowland forest, Panama to southern Mexico.

CANAL ZONE: Barro Colorado Island, *Starry* 271. PANAMÁ: Taboga Island, *Woodson*, *Allen & Seibert* 1521.

The species has not been reported previously south of Mexico, having been confused locally with *X. pilosum*, which it much resembles. The specimens, however, seem to represent a distinct species, and agree perfectly with a photograph of the type of *X. mexicanum*.

9. *DIEFFENBACHIA* Schott

DIEFFENBACHIA Schott, Wien. Zeitschr. Kunst 3:820. 1829.

Plants low or rather tall, terrestrial, the caudices thick, often elongate, prostrate, and rooting, the sap milky; petioles long, vaginate to the middle or higher, terete above; blades oblong, very thick and fleshy when living, the costa thick, disappearing toward the apex of the blade, the primary lateral nerves numerous, ascending, arcuate toward the margin, not united into a collective nerve; peduncles shorter than the leaves, the spathe oblong, persistent, the lower portion convolute, open at the throat and expanded into a spreading or recurved limb; spadix erect, slightly shorter than the spathe, often stipitiform at the base and adnate to the spathe, the pistillate portion of the spadix remotely many-flowered, the staminate part subcylindric, densely many-flowered, separated from the pistil-

late by an almost naked interval; flowers unisexual, naked; staminate flowers with 4 stamens, these connate to form a sessile, thick, 4- or 5-sulcate syndrium truncate at the apex; anthers contiguous, the cells obovoid, opening by an apical slit; pistillate flowers with 4-5 claviform staminodia, these rounded at the thickened apex, longer than the ovary, spreading; pistil 2- or 3-carpellate, sessile, depressed-ovoid, 2- or 3-lobate, 2- or 3-celled, sometimes 1-carpellate; ovules 1 in each cell, erect, anatropous; style none, the stigma 2- or 3-lobate, concave in the middle, the lobes thick; fruit baccate, 2- or 3-lobate or globose, crowned by the remnants of the stigma, 1- to 3-celled, the cells 1-seeded; seeds globose or ovoid, the testa thick, smooth; endosperm none.

The group consists of about 27 species, in Central and South America, six of them reported from Central America. The plants grow chiefly in damp or often very wet forest, where they sometimes form large, dense stands. When cut or crushed, they emit a strong, mephitic odor. The milky or yellowish sap is abundant, and is reported everywhere to cause serious irritation if it comes into contact with the skin. In the forest one often finds scattered plants whose normally green leaves are blotched with white or pale yellow. Such plants, as well as the normal green-leaved ones, have been introduced into cultivation in the North, and are sometimes seen as house plants. To such greenhouse plants the name "Mother-in-law Plant" has sometimes been given in the United States, an allusion to the fact that if a piece of the leaf is chewed (a rather dangerous experiment), sensation in the tongue is destroyed temporarily, sometimes with loss of the power of speech. The ripe fruits of all or most species are bright red at maturity, suggesting those of the "Jack-in-the-pulpit" (*Arisaema*) of the United States, a member of the same family. About the Canal Zone the Dieffenbachias are called *Otó de Lagarto*, and by the West Indians "Dumb Cane," the derivation of the latter being similar to that of "Mother-in-law Plant."

- | | |
|--|-------------------|
| a. Sheath of the petiole extending almost to the base of the leaf blade.
Spathe green..... | 1. D. PITTIERI |
| aa. Sheath of the petiole ending far below the base of the leaf blade. | |
| b. Spathes green, about 30 cm. long..... | 2. D. LONGISPATHA |
| bb. Spathes yellow or orange at maturity, mostly less than 20 cm. long. | |
| c. Leaf blades rounded at the base, the primary lateral nerves 6-9
on each side..... | 3. D. OERSTEDII |
| cc. Leaf blades cordate at the base, the primary lateral nerves about
18 on each side | 4. D. AURANTIACA |

1. DIEFFENBACHIA PITTIERI Engler & Krause, Pflanzenreich IV. 23Dc:42. 1915.

Caudex thick; petioles fleshy, 10-13 cm. long, the sheath thin-coriaceous, persistent, 10-12 mm. wide on each side, slightly narrowed above and rounded at its apex, produced almost to the base of the blade; blades rather thick when dried, obliquely lance-oblong, 18-22 cm. long, 6.5-8 cm. wide, short-acuminate, obtuse or subacute at the base, the primary lateral nerves about 8-10 on each side, very oblique, rather prominent beneath; peduncles terete, 4-5 cm. long; spathes thin and subherbaceous when dried, 20 cm. long or more, the lowest portion 1.5 cm. thick, the limb oblong-lanceolate, cuspidate-acuminate, about 8 cm. long and 3-4

cm. wide; spadix adnate for half its length to the spathe, the lowest part naked, the staminate and pistillate portions separated by a sterile or naked interval 3 cm. long, the staminate portion of the spadix 6–7 cm. long, densely flowered; ovaries depressed-ovoid, 2–2.5 mm. in diameter; synandria 2–2.5 mm. in diameter.

Endemic in Panama.

CANAL ZONE: along trail between Gamboa and Las Cruces, 50–80 m., *Pittier 3766* (U. S. Nat. Herb., TYPE). COCLÉ: El Valle, 800–1000 m., *Alston & Allen 1839*.

The species is easy of recognition because of the form of the sheaths.

2. *DIEFFENBACHIA LONGISPATHA* Engler & Krause, *Pflanzenreich* IV. 23Dc:44. 1915.

Caudex often elongate and prostrate, as much as 10 cm. or even more in diameter, erect at the apex and bearing several large leaves; petioles succulent, 35–40 cm. long, the sheath broad, persistent, ending 1.5–5 cm. below the base of the blade; blades rather thin when dried but thick and succulent when living, mostly oblong-elliptic, short-acuminate or rounded and apiculate at the apex, more or less oblique and acute to almost rounded at the base, 30–60 cm. long and 18–30 cm. wide or even larger, the primary lateral nerves 20–22 on each side, divergent at an angle of 45–60 degrees; peduncles 20–25 cm. long, 1 cm. thick; spathe large, coriaceous, 30 cm. long or more, orange or yellow, the convolute portion 20 cm. long, the limb oblong, 4 cm. wide; lowest part of the spadix naked, the pistillate remotely few-flowered, reaching to the middle of the spathe or higher, the staminate part of the spadix separated from the pistillate by a sterile interval; ovary broadly depressed, 4–5 mm. in diameter, the staminodia linear, 5 mm. long.

Wet or swampy woods, lowlands of Panama.

COLÓN: Fató (Nombre de Dios), on marshy, alluvial flats, *Pittier 3838* (TYPE). PANAMÁ: Río Tapia, *Standley 28156, 26238*. CANAL ZONE: Fort Randolph, *Standley 28732*; hills between Río Grande and Pedro Vidal, 50–150 m., *Pittier 2715*.

This species is noteworthy for its unusually large leaves and spathes, which in size exceed those of all other Central American species.

3. *DIEFFENBACHIA OERSTEDII* Schott, *Oesterr. Bot. Zeitschr.* 8:179. 1858.

Caudex usually erect, sometimes decumbent, as much as a meter high, and often very thick; petioles 12–20 cm. long, succulent, slender and terete above the sheath, the sheath about two-thirds as long as the petiole; blades oblong-ovate, thin when dried but succulent in the living state, 12–30 cm. long, 6–14 cm. wide, short-cuspidate or short-acuminate, rounded or truncate at the base, the primary lateral nerves slender, 6–9 on each side; peduncles slender, 8–11 cm. long; spathes yellow or orange at maturity, about 15 cm. long and 3–4 cm. wide, lance-oblong; lower part of the spadix naked, the pistillate portion 5 cm. long, the staminate of the same length, fusiform, 10–12 mm. thick at the middle, the two separated by a sterile interval of 2 cm.; berries bright red.

Damp or wet forest, Panama to Guatemala; in Panama at or near sea level.

CANAL ZONE: Barro Colorado Island, *Standley* 31266, 40960, 41107; *Kenoyer* 188; *Maxon* 6812, 6820; Gamboa, *Pittier* 2600; Frijoles, *Pittier* 3754; above East Paraiso, *Standley* 29867. COLÓN: Loma de la Gloria, near Fató, *Pittier* 3847. CHIRIQUÍ: near David, *Pittier* 2836. BOCAS DEL TORO: Cocoa Cay, Chiriquí Lagoon, *Wedel* 2892.

4. *DIEFFENBACHIA AURANTIACA* Engler, Bot. Jahrb. 26:566. 1899.

Plants coarse and stout, about a meter high, with a thick, erect caudex; petioles half as long as the blades or often much shorter, thick and succulent, vaginate to above the middle and often almost to the base of the blade; blades often spotted with white or pale yellow, oblong to oblong-ovate, 25–40 cm. long and 9–20 cm. wide or larger, acuminate, shallowly and broadly cordate at the base, the primary lateral nerves usually 12–18 on each side, the lowest divergent at almost a right angle; inflorescences numerous, the slender peduncles mostly 4–7 cm. long; spathes pale yellow to orange or greenish yellow, 14–25 cm. long, at the base 1.2–3.5 cm. broad, gradually long-attenuate; pistillate portion of the spadix in fruit as much as 18 cm. long; berries orange-red at maturity, numerous and densely crowded, subglobose.

Usually in dense, wet forest at or near sea level, Costa Rica and Panama.

CANAL ZONE: hills north of Frijoles, *Standley* 27413; between Frijoles and Monte Lirio, *Killip* 12154; lake shore along Gatún River, *Pittier* 6845; Barro Colorado Island, *Bailey* 335. BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, *Woodson*, *Allen* & *Seibert* 1909; Water Valley, Chiriquí Lagoon, *Wedel* 1438. CHIRIQUÍ: Puerto Armuelles, *Woodson* & *Schery* 861.

10. *RHODOSPATHA* Poepp.

RHODOSPATHA Poepp. in Poepp. & Endl. Nov. Gen. Sp. 3:91. 1845.

Plants epiphytic, more or less scandent and rooting at the nodes; leaves distichous, the petiole about equaling the blade, long-vaginate, geniculate below the base of the blade; blades oblong to oblong-elliptic, slightly unequal at the base, the primary and secondary lateral nerves numerous, slender, subparallel, spreading or acutely ascending, arcuate near the margin; peduncles much shorter than the leaves, the spathe broadly ovate or oblong-ovate, abruptly cuspidate, longitudinally nerved, greenish outside, white or pink within, soon deciduous; spadix stipitate or sessile, cylindric, densely many-flowered, sometimes with only pistillate flowers at the base, but most of the flowers perfect; flowers naked, the stamens 4, the filaments rather broad, complanate, narrowed to the slender, acuminate connective; anthers rather broad, the cells elliptic, longer than the connective, dehiscent by lateral slits; ovary 4-angled, 2-celled, the ovules several or numerous in each cell, amphitropous; style thicker than the ovary, the stigma linear or rarely 2- or 3-lobate; berries small, cylindric-prismatic, truncate, 10- to 12-seeded; seeds attached by short funicles, vertically imbricate, rounded-reniform, lentiform, the testa minutely verruculose.

A genus of a dozen species, widely dispersed in tropical America. Four species are recorded from Central America.

1. *RHODOSPATHA FORGETI* N. E. Brown, Kew Bull. 358. 1913.

Caudex scandent; petioles slender, 30–35 cm. long, narrowly vaginate to the node, the margins of the sheath entire; blades oblong-lanceolate, commonly 40–50 cm. long and 11–15 cm. wide, cuspidate-acuminate, cuneate at the base, thin, green above, somewhat paler beneath, the lateral nerves very numerous and slender, all subequal, ascending at an angle of about 45 degrees; peduncles 12–15 cm. long; spathe 13–15 cm. long, 9–10 cm. wide when expanded, broadly elliptic, pinkish white outside, dirty pink within, cuspidate-acuminate; spadix white, short-stipitate, 8–12 cm. long, becoming 1.5 cm. thick, obtuse, pale pinkish; ovaries 3 mm. long, 4- or 5-angulate; ovary cells many-ovulate.

Described from cultivated plants of Costa Rican origin. Known otherwise only from the Panama material cited here.

CANAL ZONE: Barro Colorado Island, *Standley 40959, 41143*. DARIÉN: Crest, Cana-Cuasi trail, Chepigana District, 1650 m., *M. E. & R. A. Terry 1553*.

I have seen no authentic representation of *R. Forgeti*, but the first collection cited agrees well with the original description. It is rather probable, however, that *R. Forgeti* is synonymous with the earlier *R. Wendlandii* Schott, also Costa Rican.

11. HOMALONEMA Schott

HOMALONEMA Schott, Melet. 20. 1832.

Plants terrestrial, the short caudex epigeal or rarely hypogean; petioles usually longer than the blades, vaginate below, the blades membranaceous or herbaceous, glabrous or pubescent, commonly cordate or sagittate; peduncles several, shorter than the petioles; spathe usually greenish, convolute below, open above, persistent; spadix stipitate or sessile, slightly shorter than the spathe, the pistillate portion cylindroid, comprising half or less of the total length, the staminate portion contiguous with the pistillate; staminate flower with 2–4 or rarely 6 stamens, these short, truncate at the apex, the anther cells ovoid or oblong, equaling or longer than the filament, opening by an oval, apical pore; pistillate flowers 2- to 4- or rarely 5-gynous, the pistil ovoid to oblong or subglobose; ovary incompletely 2- to 4-celled, the ovules numerous; stigma sessile, discoid, orbicular or shallowly 2- to 4-lobate; berries obovoid to oblong or subglobose, incompletely 2- to 5-celled, the cells many-seeded; seeds attached by a long funicle, ellipsoid or elongate-ellipsoid, blackish brown, longitudinally striate.

The genus consists of about 80 species, chiefly in the Old World. The following is the only North American one.

1. HOMALONEMA WENDLANDII Schott, Prodr. Aroid. 308. 1860.

Plants rather large and robust, the caudex hypogean; petioles 40–50 cm. long, vaginate for a third their length, terete above and 4–5 mm. thick, densely puberulent; blades dark green above, reddish-margined, paler beneath, sagittate or cordate-sagittate, 30–50 cm. long, 20–30 cm. wide, acute or short-acuminate, glabrous above, puberulent beneath, at least on the nerves, the basal lobes semi-ovate or subtriangular, separated by a broad or narrow sinus, the costal lateral

nerves 10-14 on each side, curved near the margin; peduncles 5-10 cm. long, densely puberulent, almost 1 cm. thick; spathe brownish outside, spotted with yellow, whitish within, the lower convolute portion 8 cm. long and 4 cm. broad, the blade 15 cm. long, 6-7 cm. wide, with a cusp 2.5-3 cm. long; spadix sessile, the pistillate portion 5 cm. long, 2 cm. thick, green, the staminate part subconoid, 12 cm. long, 1.5 cm. thick at the base, gradually attenuate to the apex; staminate flowers with 5 stamens; pistil ovoid, subtetragonous, the stigma shallowly 4-lobate; fruiting inflorescence 10 cm. long or more and 5 cm. thick; berries 12 mm. long, 5 mm. thick.

Described from plants of Costa Rican origin cultivated in Berlin; lowland forests of Panama.

CANAL ZONE: Matachin, *Cowell* 203; Barro Colorado Island, *Kenoyer* 189.

The plant is easy of recognition because of its combination of terrestrial habit and pubescent blades, petioles, and peduncles.

12. ANEPSIAS Schott

ANEPSIAS Schott, Gen. Aroid. *pl.* 73. 1858.

Large, scandent epiphytes, the leaves distichous; petioles long, vaginate almost to the apex, the sheath persistent, adnate for its whole length; blades obliquely ovate-oblong, very large, thin when dried, the primary lateral nerves numerous, spreading, the secondary nerves parallel with them, the veins reticulate; inflorescence terminal, solitary, the peduncle much shorter than the petiole, stipitiform above the base of the spathe; spathe oblong, acuminate, convolute, deciduous in fruit; spadix long and slender, slightly shorter than the spathe, very densely many-flowered; flowers perfect, naked; stamens 4, the filaments short, complanate, abruptly narrowed at the apex to the slender, acuminate connective; anthers shorter than the filaments, the cells elliptic, exceeding the connective, apiculate, dehiscent by elongate, lateral slits extending to the base of the anther; ovary obpyramidal, prismatic, truncate, 2- to 6-celled; ovules numerous in the cell, anatropous, erect or spreading, 2- to 6-seriate; style as thick as the ovary, the stigma linear.

The genus consists of a single species.

1. ANEPSIAS MORITZIANUS Schott, Gen. Aroid. *pl.* 73. 1858.

A large, epiphytic vine, the caudex rooting at the nodes, the internodes 1 cm. long and thick; petioles 30-40 cm. long or more, 2-2.5 cm. broad at the base, slender above; blades 30-65 cm. long and 15-30 cm. wide or even larger, abruptly short-acuminate, rounded and abruptly short-decurrent at the base or cuneately acute, the primary lateral nerves about 20 on each side, very slender but prominent beneath; peduncles about 15 cm. long, rather stout, the spathe 15-19 cm. long, 6-7 cm. wide; spadix 13-18 cm. long, borne on a stipe 1 cm. long, 1-1.5 cm. thick near the base, very slightly narrowed to the obtuse apex, white at maturity; ovaries scarcely 3 mm. long and 1 mm. thick.

Originally described from rain forests of Tovar, Venezuela, and known otherwise, apparently, only from Santa María de Dota, Costa Rica, and Panama.

CANAL ZONE: Barro Colorado Island, *Standley* 31462; *Aviles* 36; between Frijoles and Monte Lirio, in forest, *Killip* 12153. CHIRIQUI: vicinity of San Bartolomé, Peninsula de Burica, *Woodson & Schery* 929.

13. STENOSPERMATION Schott

STENOSPERMATION Schott, Gen. Aroid. 70. 1858.

Plants epiphytic, rooting at the nodes and more or less scandent, densely leafy,



Fig. 88. *Stenospermation sessile*

the leaves distichous; petioles long-vaginate, geniculate below the base of the blade; blades oblong-elliptic or lanceolate, unequal-sided, rather coriaceous when dried, very succulent when living, the primary lateral nerves numerous, obliquely ascending; peduncles rather long, nutant at first at the apex, later erect; spathe convolute, open in anthesis, whitish, soon deciduous; spadix sessile or stipitate, cylindric, whitish; flowers perfect and fertile, naked; stamens 4, the filaments complanate, abruptly narrowed at the apex into the slender connective, equaling the ovary; anther cells oblong-ovoid, acute, dehiscent by lateral slits that do not reach the base of the cell; ovary obpyramidal or prismatic, truncate at the apex, 2-celled; ovules 4 or more in each cell, collateral, anatropous; style short, thicker than the ovary, the stigma linear-oblong; fruits small, baccate, obovoid, subtruncate at the apex, 2-celled, each cell with 3 or

more seeds; seeds clavate-cylindric, slender, with a rather thick testa; endosperm copious.

A genus of about 20 species in tropical America. Six species are recorded for Central America.

- | | |
|---|-------------------------|
| a. Spadix sessile..... | 1. <i>S. SESSILE</i> |
| aa. Spadix conspicuously stipitate..... | 2. <i>S. SPRUCEANUM</i> |

1. STENOSPERMATION SESSILE Engler, Bot. Jahrb. 37:111. 1905.

A small or large vine, almost frutescent, the caudex commonly 1 cm. thick, sometimes as much as 2 cm., the internodes short; petioles 6–25 cm. long, the

sheath broad at the base, narrowed upward, ending 1-3 cm. below the base of the blade; blades oblong or lance-oblong, mostly 13-18 cm. long and 3-5 cm. wide, acuminate or long-acuminate, acute at the base; peduncles slender, 12-30 cm. long; spathe oblong, short-acuminate, white, about 4 cm. long, 1 cm. wide, early deciduous; spadix sessile, cylindric, obtuse, 2.5-3.5 cm. long, 5-8 mm. thick, pale green or yellow.

Costa Rica and Panama, epiphytic on trees in dense forests, usually at or near sea level.

CANAL ZONE: Balboa, cultivated, *Standley 28548*; Barro Colorado Island, *Standley 41147*; Río Indio de Gatún, *Pittier 5735*; Quebrada López, *Allen 2140*. COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2198*. BOCAS DEL TORO: Little Bocas, *Wedel 2536*.

In Panama this species probably is confined to the Atlantic lowlands, but it may well be expected in the mountains of Chiriquí, since in Costa Rica it ascends to 1,600 meters and higher. The plant may be recognized by the rather thick and flexible-leathery (when dried) leaves, with very numerous but obscure, oblique nerves. Noteworthy also for the short, very blunt spadix, and the deciduous spathe. Illustrated, Engler, *Pflanzenreich* IV. 23B: fig. 34, J-M.

2. STENOSPERMATUM SPRUCEANUM Schott, Gen. Aroid. 70, fig. 1-14. 1858.

Caudex elongate, as thick as a finger, the internodes 5-10 mm. long; petioles of the lower leaves 8-25 cm. long, vaginate almost to the apex; blades coriaceous, oblong-elliptic or oblong-lanceolate, 15-26 cm. long, 5-7 cm. wide, subacuminate to very obtuse and apiculate at the apex, the primary lateral nerves about 20 on each side, ascending at a very narrow angle; peduncles slender, 18-30 cm. long; spathe ovate-oblong, acuminate, 8-11 cm. long, pale green; spadix borne on a stipe 5 mm. long, cylindric, very obtuse, 3.5-4 cm. long, 7-8 mm. thick; pistils short-turbinate, 1 mm. long and broad, tetragonous at the apex.

Wet forest, Panama to Colombia, British Guiana, and Amazonian Peru.

DARIÉN: Cerro de Garagará, Sambú Basin, 500-970 m., *Pittier 5674*. COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2197*.

The first collection cited was determined by Engler and Krause as perhaps referable to this species. It agrees well enough with South American material, and probably can be referred permanently to *S. Spruceanum*.

14. SYNGONIUM Schott

SYNGONIUM Schott, Wien. Zeitschr. Kunst 3:780. 1829.

Scandent epiphytes, the caudices often greatly elongate, the internodes mostly long, the nodes emitting roots; earliest leaves ovate, the next sagittate, the adult ones trisect or pedatisect; petioles long, terete above, rather long-vaginate; blades varying from trisect to pedately 5- to 9-cleft, the primary lateral nerves of the segments spreading, forming 1-3 collective nerves; peduncles usually clustered, equaling or shorter than the spathe, pendent or recurved in fruit; spathes pale or yellowish green, rarely purplish, in fruit often turning bright red, the tube ovoid,

slightly exceeding the pistillate inflorescence, the limb oblong-ovate, erect-spreading and open at anthesis, usually deciduous in fruit; spadix much shorter than the spathe, the pistillate inflorescence oblong-conoid, the staminate portion of the spadix longer than the pistillate, clavate, sterile at the base; flowers unisexual, naked; staminate flowers with 3-4 stamens, these connate to form a truncate-obpyramidal, 3- or 4-sided synandrium; connective of the anthers thick, the cells rounded or obtuse at the base, dehiscent below the apex of the connective by a short slit; pistillate flowers connate, the ovary obovoid or oblong-obovoid, normally 2-celled, by abortion sometimes 1-celled; ovules 1 in each cell, erect, anatropous; stigma convex or hemispheric, sometimes 2- or 3-emarginate; fruits baccate, connate into an ovoid syncarp; seed obovoid, borne on a very short funicle, the testa smooth, thin, black; endosperm none.

A genus of about 15 species, confined to tropical America. Seven species are known from Central America.

- a. Adult leaves trisect 1. *S. HOFFMANNII*
 aa. Adult leaves 5- to 11-cleft 2. *S. PODOPHYLLUM*

1. *SYNGONIUM HOFFMANNII* Schott, Oesterr. Bot. Zeitschr. 8:178. 1858.

Porphyrospatha Hoffmannii (Schott) Engler in DC. Monogr. Phan. 2:291. 1879.



Fig. 89. *Syngonium Hoffmannii*

Probably a large vine; petioles very slender, 20-30 cm. long, the narrow sheath 13-18 cm. long, adnate for its whole length; blades trisect, the middle segment ovate-oblong to elliptic, 15-18 cm. long, 6-11 cm. wide, acuminate, cuneately narrowed to the sessile base, the primary lateral nerves 5-6 on each side, united to form a collective nerve rather remote from the margin, the lateral segments oblong or obliquely ovate, slightly smaller than the middle one, sometimes subauriculate on the outer side, short-petiolulate; peduncles slender, about 7 cm. long, recurved; spathe subcoriaceous, whitish outside, turning orange, pale purple within, the tube oblong-ovoid, 4.5-8 cm. long, adnate to the stipe, the blade ovate-oblong, 7-8 cm. long, 6 cm. wide, caudate-acuminate; spadix slightly more than half as long as the spathe, the pistillate portion 2.5 cm. long, 1.5 cm. thick, the staminate portion cylindric, very obtuse, 5 cm. long and almost 2 cm. thick at maturity; stamens 4, the synandria 1.5 mm. long;

pistils obovoid, 1 mm. long, the stigma discoid, bilobate.

Forests of Costa Rica (described from Candelaria, near San José) and the Pacific slope of Panama.

CHIRIQUÍ: Río Chiriquí to Remedios, 15-50 m., *Woodson, Allen & Seibert 1189*; San Bartolomé, Península de Burica, *Woodson & Schery 930*.

2. *SYNGONIUM PODOPHYLLUM* Schott, Syn. Aroid. 68. 1856.

Syngonium salvadorens Schott, Oesterr. Bot. Zeitschr. 8:178. 1858.

Syngonium Oerstedianum Schott, Oesterr. Bot. Zeitschr. 8:178. 1858.

A large, epiphytic vine, the caudex 1-1.5 cm. thick, the internodes elongate; juvenile leaves long-petiolate, the blades sagittate, 13-15 cm. long, the basal lobes triangular or oblong-lanceolate, the terminal lobe acuminate; petioles of adult leaves 40-50 cm. long, vaginate for about half their length, the blades 5- to 11-cleft, the middle segment of the blade about 20 cm. long and 6-7 cm. wide, the next lateral segments slightly shorter and narrower, the outermost about 10 cm. long, often auriculate on the outer side, the segments separated by short or elongate internodes of the rachis; peduncles several, separated by linear-lanceolate, whitish cataphylls, about 10 cm. long; tube of the spathe 3-5 cm. long and 1.5-2 cm. thick, oblong-ovoid, the blade about 6 cm. long and 4-5 cm. wide, green outside, whitish or pink within, ovate, cuspidate; pistillate portion of the spadix 2 cm. long, green, the staminate 5 cm. long, 10-13 mm. thick, slightly attenuate to each end; ovaries depressed-obpyramidal, the stigma discoid, suborbicular.

Climbing over trees in wet forest, or often in exposed and rather dry places, Panama to southern Mexico.

CANAL ZONE: common in forests and doubtless general through the moist lowlands, or even extending well up into the mountains. BOCAS DEL TORO: Johns Creek, Chiriquí Lagoon, *Wedel 2765*; Darkland, Chiriquí Lagoon, *Wedel 2616*.

The mature fruiting spathes are usually bright red, and cause the plant to be even more conspicuous than it would otherwise be even with its unusual and decorative foliage. It is now rather frequent in cultivation in Florida and other warm parts of the United States, and has become popular also as a house plant, for its succulent leaves withstand well the trying conditions of steam-heated apartments. It has been discussed and illustrated recently by L. H. Bailey (*Gentes Herb.* 4:305-308. 1940). Illustrated also by Engler, *Pflanzenreich* IV. 23E:126. 1920.

15. *PHILODENDRON* Schott

PHILODENDRON Schott, Wien. Zeitschr. Kunst 3:780. 1829.

Plants usually epiphytic and scandent, the internodes mostly elongate, the nodes often emitting roots; petioles short or elongate, rarely geniculate near the apex, vaginate for part or all their length; blades herbaceous or more or less coriaceous, very variable in form, sometimes lobed or parted, the lateral nerves all parallel and equal, or the primary ones often stouter than the secondary; peduncles generally short; spathes succulent, mostly whitish, yellowish, or red, the tube convolute, cylindric or ventricose, persistent, the blade cymbiform, ovate to lanceolate, commonly erect and after fecundation reconvolute, persistent in fruit; spadix

almost equaling the spathe, sessile or short-stipitate, the pistillate portion cylindric, densely many-flowered, juicy in fruit, the staminate portion sterile below, fertile above for most of its length, finally drooping in fruit; flowers unisexual, naked; stamens of the staminate flower 2-6, sessile, obpyramidal-prismatic, truncate at the apex, the anther cells oblong or linear, emarginate at the base, opening by a short slit; ovary of the pistillate flower obovoid or ovoid, 2- to several-celled; ovules orthotropous or half-anatropous, ascending on rather long funicles, few or numerous; stigma sessile, hemispheric or sometimes lobulate; fruits baccate, densely crowded; seeds rather numerous, few, or only 1, ovoid-oblong or ellipsoid, straight, the testa rather thick, striate-costate; endosperm present.

The second-largest American genus of *Araceae*, with 200 or more species. They are distributed over most of tropical America, but are most numerous in the Andean region. About 28 species are known from Central America.

Plants of this genus constitute a large and conspicuous element of the epiphytic vegetation of the Panama lowlands. The leaves of many species are handsome and attractive. Various species of *Philodendron* may be seen commonly in northern greenhouses, and a few are cultivated as house plants.

- a. Leaf blades lobed or variously parted.
 - b. Leaves 3-parted, the segments oblong, entire..... 1. *P. TRIPARTITUM*
 - bb. Leaves pinnatifid, with numerous narrow lobes..... 2. *P. RADIATUM*
- aa. Leaf blades entire.
 - b. Leaves deltoid-cordate, rounded-cordate, oblong-cordate, or sagittate-cordate, deeply cordate at the base, with a broad or narrow sinus and well-developed posterior lobes.
 - c. Petioles glabrous.
 - d. Basal sinus of the leaves very broad and open, much wider than long, the basal lobes slightly spreading outward. Blades large, mostly 30-50 cm. long or larger, the primary lateral nerves much stouter than the secondary ones..... 3. *P. PANAMENSE*
 - dd. Basal sinus of the leaves deep and narrow, normally much longer than broad, the basal lobes directed downward or even slightly inward.
 - e. Primary lateral nerves of the leaves little or not at all stouter than the parallel secondary ones; blades large and thin, mostly more than 30 cm. long..... 4. *P. GRANDIPES*
 - ee. Primary lateral nerves of the leaves conspicuously stouter and more prominent than the secondary ones; blades mostly less than 25 cm. long.
 - f. Leaves thin when dried, oblong-cordate; spathes 6-7.5 cm. long..... 5. *P. BREVISPATHUM*
 - ff. Leaves thick and rather coriaceous when dried, broadly cordate or rounded-cordate; spathes about 12 cm. long.
 - g. Basal sinus broadly obtuse; primary lateral nerves of the leaves 4-5 on each side..... 6. *P. HOFFMANNII*
 - gg. Basal sinus acute; primary lateral nerves of the leaves about 10 on each side..... 7. *P. BRENESII*
 - cc. Petioles covered with long, soft, hair-like setae..... 8. *P. VERRUCOSUM*
 - bb. Leaves various in shape but never cordate or sagittate, acute to rounded at the base or, if shallowly cordate, oblong and without evident basal lobes.
 - c. Leaf blades evidently cordate at the base or rarely rounded (in juvenile leaves), usually broadest above the middle..... 9. *P. WENDLANDII*
 - cc. Leaf blades truncate to acute at the base, broadest at or below the middle.
 - d. Sheath of the petiole ending far below the base of the blade. Leaf blades elliptic-oblong, usually narrowed to the base, this

- often subacute but sometimes broadly rounded..... 10. *P. KARSTENIANUM*
 dd. Sheath of the petiole extending nearly or quite to the base of
 the blade.
 e. Primary lateral nerves of the leaves much stouter and more
 conspicuous than the secondary ones; leaf blades large, usually
 25-35 cm. long or more..... 11. *P. COERULESCENS*
 ee. Primary lateral nerves of the leaves little stouter or more con-
 spicuous than the secondary ones; leaf blades mostly 20 cm.
 long or less 12. *P. GUTTIERUM*

1. *PHILODENDRON TRIPARTITUM* (Jacq.) Schott, Melet. 1:19. 1832.

Arum tripartitum Jacq. Hort. Schoenbr. 2:33, pl. 190. 1797.

A small or large, epiphytic vine, the internodes elongate, 5-12 cm. long, 1-1.5 cm. thick; cataphylls elongate-lanceolate, caducous; petioles terete, commonly 20-30 cm. long and 1-1.5 cm. thick at the base; blades thin when dried, 3-parted, the segments oblong-lanceolate, acuminate or short-cuspidate, subequal, about 15-25 cm. long and 4-7 cm. wide, the lateral ones conspicuously oblique, all 3 segments sessile, almost or quite distinct; peduncles solitary, 3-7 cm. long, rather stout; spathe whitish, toward the apex often yellowish, the tube oblong, 3-4 cm. long, the blade ovate or ovate-oblong, short-acuminate, about 5-6 cm. long and 3 cm. wide; spadix borne on a stipe 2-4 cm. long, the pistillate portion 3-4 cm. long, 8-10 mm. thick, the staminate 3.5-5 cm. long, slightly attenuate upward; pistils cylindric, 1.5-1.8 mm. long, 7- to 11-celled, the cells 1- or 2-ovulate; berries red.

Climbing over trees, usually in wet forest, commonly at or near sea level, British Honduras and Guatemala to Jamaica, Venezuela, and Colombia. Originally described from Caracas, Venezuela.

CANAL ZONE: Frijoles, *Pittier* 3755; Barro Colorado Island, *Sbattuck* 182. PANAMÁ: Juan Díaz, *Standley* 30618.

Pittier 5601 from Garagará, cited by Engler and Krause under this species (*Pflanzenreich* IV. 23Db:108. 1913), is rather *Anthurium garagaranum* Standl. Illustrated, *Pflanzenreich* IV. 23Db:108.

2. *PHILODENDRON RADIATUM* Schott, Oesterr. Bot. Wochenbl. 3:378. 1853.

A large, epiphytic vine, the caudex sometimes 12 cm. or even more in diameter, the lower internodes 10 cm. long, the upper ones 2-3 cm. long; cataphylls pale pink, linear-lanceolate; petioles terete, at least above, 40-65 cm. long, almost 2 cm. thick at the base; blades coriaceous when dried, very fleshy when growing, the earliest juvenile ones ovate-oblong and subentire, the later ones shallowly or deeply incised-lobate, the adult blades ovate-cordate in outline, 35-55 cm. long and 30-35 cm. wide or often much larger, with 5-10 segments on each side, these lanceolate to linear-lanceolate, often again lobate, acuminate, the middle segments 2-2.5 cm. wide, the basal ones much shorter and coherent; peduncles 4-5 cm. long; spathes about 20 cm. long, green outside or somewhat purplish, whitish and purplish within, cymbiform, the blade equaling or slightly longer than the tube; spadix 12-18 cm. long, the pistillate portion cylindric, the staminate terete-conoid, obtuse, slightly longer than the pistillate portion; pistils pale green, oblong, 2-3

mm. long, 8- to 10-celled, crowned by the rounded stigma, the cells 4- or 5-ovulate; stamens 4-6; berries oblong, 6-7 mm. in diameter.

Climbing over trees in moist or wet forest, southern Mexico to Panama, at or near sea level, or in some parts of Central America ascending to 700 meters.

CANAL ZONE: between Gorgona and Gatún, *Pittier* 2300; Barro Colorado Island, *Shattuck* 266; *Kenoyer* 178a; *Standley* 31328, 40818; near Fort Sherman, *Standley* 30902; near Fort Randolph, *Standley* 28626; near Gatún, *Standley* 27203; hills north of Frijoles, *Standley* 27467. BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, *Woodson, Allen & Seibert* 1901.

Local names are *Azota-cabeza* and *Chaldé*. *Pittier* 2300 was reported by Engler and Krause (Pflanzenreich IV. 23Db:121. 1913) as *Philodendron Warszewiczii* C. Koch, a species of Guatemala and Salvador, evidently in error. Illustrated, Pflanzenreich IV. 23Db: fig. 40.

3. PHILODENDRON PANAMENSE Krause, Pflanzenreich IV. 23Db:65. 1913.

A large, epiphytic vine, doubtless with a thick caudex; petioles rather stout, terete, as much as 50 cm. long, at the base 1.5 cm. thick, attenuate upward; blades rather thick and coriaceous when dried, usually triangular-ovate-cordate, 30-50 cm. long and 25-30 cm. wide, or often much larger, almost obtuse at the apex and obliquely short-cuspidate, the basal lobes rounded or rounded-obtuse, often slightly spreading outward, separated by a rather shallow, very broad sinus, the primary costal nerves 6-7 on each side, divergent at a wide angle, much stouter than the secondary nerves; peduncles 12-15 cm. long, stout; spathe white or whitish, or in fruit red, the tube ovoid, 5 cm. long and 3 cm. broad, the blade oblong, as much as 8 cm. long, acute; spadix sessile, the pistillate portion subovoid or ellipsoid, 5-7 cm. long, 2 cm. or more in diameter, the staminate portion cylindric, about as long as the pistillate, 12 mm. thick; pistils ovoid-oblong, 3-3.5 mm. long, 2 mm. broad, 5- or 6-celled, crowned by the orbicular stigma.

Climbing over trees in wet forest, at or near sea level, Panama; perhaps also in Costa Rica.

CANAL ZONE: Frijoles, *Pittier* 3753 (TYPE); between Frijoles and Monte Lirio, *Killip* 12133; Barro Colorado Island, *Starry* 47; *Aviles* 25, 46; L. H. & E. Z. *Bailey* 199; *Kenoyer* 184, 185; Fort Randolph, *Standley* 28728.

The local name is reported as *Bejuco Lengua de Vaca*. *Aviles* 46, from Barro Colorado, consists of a single leaf, noteworthy for being oblong-hastate, with a rather narrowly oblong anterior division and large basal lobes. It is probably no more than a juvenile leaf form.

4. PHILODENDRON GRANDIPES Krause, Pflanzenreich IV. 23Db:48. 1913.

A scandent epiphyte, perhaps sometimes terrestrial and acaulescent or nearly so(?); petioles long and very slender, 40-65 cm. long; blades thin when dried and usually somewhat fuscous, rounded-ovate-cordate, 27-40 cm. long, 20-25 cm. wide, short-cuspidate, deeply cordate at the base, the basal lobes broadly rounded or obtusely angulate, directed downward, the sinus deep and narrow but open, the primary costal nerves about 10 on each side, divergent at a wide angle, con-

spicuously stouter than the secondary nerves but nevertheless very slender; peduncles terete, slender, 8–10 cm. long; spathe green, the tube 3 cm. long, 2.5 cm. thick, the limb ovate-oblong, short-acuminate, 4–4.5 cm. long, 2.5–3 cm. wide when expanded; spadix short-stipitate, the pistillate portion cylindric, 2.5 cm. long, almost 1 cm. thick, the staminate part subclavate, 4 cm. long, 8–10 mm. thick at the middle, attenuate to each end, acutish; pistils prismatic, 1.8 mm. long, 4- to 6-celled, capped by the rounded stigma; cells of the ovary many-ovulate.

Climbing over trees in wet forest, at or near sea level, Panama.

COLÓN: Dos Bocas, Río Fató valley, Pittier 4228 (TYPE). CANAL ZONE: Barro Colorado Island, Standley 31361, 40888; hills north of Frijoles, Standley 27471; Gamboa, Standley 28401.

5. *PHILODENDRON BREVISPATHUM* Schott, Bonplandia 7:29. 1859.

Caudex with slender, elongate internodes; petioles subterete, 16–18 cm. long, short-vaginate; blades oblong-cordate, 20–27 cm. long, 6–12 cm. wide, acuminate, deeply cordate at the base, the basal lobes rather narrow, rounded, directed downward, the sinus deep and narrow, the primary costal nerves 5–6 on each side, much stouter and more prominent than the secondary ones; peduncles 1–2 cm. long; tube of the spathe globose-ventricose, 3 cm. long, the limb yellow, broadly ovate, cuspidate-acuminate, equaling or slightly exceeding the tube; spadix borne on a stipe 3–4 mm. long, the pistillate portion 2–2.5 cm. long, the staminate part cylindric, attenuate upward, up to 6 cm. long, below about 1 cm. thick; pistils oblong, 6-celled, capped by the small, rounded stigma; stamens usually 4.

Known only from the original Panama material.

CANAL ZONE: Chagres, Fendler 431.

Of this I have seen only a single specimen of the original collection, in the U. S. National Herbarium, consisting of one leaf. The leaf bears much resemblance to those of *P. panamense*, but is not matched exactly by any specimens recently collected in Panama.

6. *PHILODENDRON HOFFMANNII* Schott, Oesterr. Bot. Zeitschr. 8:178. 1858.

A large, epiphytic vine, the caudex slender, its internodes elongate; petioles subterete, 12–16 cm. long or even longer; blades thick-coriaceous when dried, broadly ovate-cordate, mostly 18–24 cm. long and 14–16 cm. wide, acuminate or long-acuminate, the basal lobes broadly rounded, directed downward, the sinus deep but usually narrow and acute, the primary costal nerves 4–5 on each side, conspicuously stouter or more conspicuous than the secondary ones; peduncles 4–5 cm. long, or sometimes twice as long or more; spathes green, cream-colored, or white, the tube ovoid, 4–5 cm. long, the limb oblong, cuspidate-acuminate, 5 cm. long or even as much as 10 cm.; spadix sessile, cream-colored or white, pistillate portion 1.5–2 cm. long and of the same thickness, the staminate part 5–5.5 cm. long, 1 cm. thick above; pistils elongate, 4 mm. long, 1 mm. thick, capped by the orbicular, discoid stigma, 3-celled; ovules 2 in each cell; stamens commonly 4.

Climbing over trees in wet or moist forest, usually near sea level, but in Guatemala ascending to 1,100 meters or more, Panama to Guatemala.

CANAL ZONE: Barro Colorado Island, *Aviles* 42; *Shattuck* 60; Fort San Lorenzo, *Maxon* 7001; France Field, *Standley* 30439. COLÓN: Porto Bello, *Pittier* 2424. PANAMÁ: near Panamá, *Standley* 26841; Río Tapia, *Standley* 28112. BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *Wedel* 1253, 2668.

Here perhaps is referable Hemsley's report (*Biol. Centr.-Amer. Bot.* 3:421. 1885) of "*P. cuspidatum* K. Koch" from Panama, on the basis of a Wagner collection. *P. cuspidatum* C. Koch & Bouché is considered by Engler and Krause a variety of *P. scandens* Koch & Sello, a West Indian species, closely related to *P. oxycardium* Schott. The Panama specimens of this alliance, although fairly numerous, are not in good condition for critical study, most of them being sterile. *Pittier* 2424 was referred by Engler and Krause doubtfully to *P. Hoffmannii*. The writer suspects that all the Panama material is perhaps better referable to *P. oxycardium* Schott. The local name of *Bejuco de Corazón* is reported for this plant.

7. *PHILODENDRON BRENESII* Standl. *Field Mus. Bot. Ser.* 18:140. 1937.

A large, epiphytic vine; petioles rather stout, subterete, 12–45 cm. long, vaginate below for 3–5 cm.; blades thick and almost subcoriaceous when dried, oblong-ovate to broadly ovate, 35–60 cm. long, 15–28 cm. wide, gradually and narrowly acuminate, deeply cordate at the base, with a rather narrow, acute sinus, the basal lobes 5–12 cm. long, rounded, directed downward, bright green and lustrous above, pale beneath and almost glaucescent, the costa thick and prominent, the primary lateral nerves about 10 on each side, slender, elevated, much stouter than the very numerous secondary nerves; spathe about 16 cm. long, 1.5 cm. thick at the base, green below, white above, the spadix of about the same length.



Fig. 90. *Philodendron verrucosum*

Scandent over trees in wet forest, at 1,000–1,700 meters, Costa Rica and Panama, the type from La Palma de San Ramón, Costa Rica.

CHIRIQUÍ: Callejón Seco, Volcán de Chiriquí, 1700 m., *Woodson & Schery* 510.

8. *PHILODENDRON VERRUCOSUM* Mathieu, *Cat.* 1854, ex Schott, *Syn. Aroid.* 85. 1856.

Plants usually terrestrial but said to be sometimes epiphytic, the caudex 2 cm. or less in diameter; cataphylls large, oblong, pink, obtuse, setose, 5–8 cm. long; petioles stout, terete or subangulate, 10–18 cm. long, dark red, cov-

ered everywhere with long soft scales or setae; blades herbaceous, broadly ovate-cordate, 15–45 cm. long, 10–30 cm. wide, acuminate, very deeply cordate at the base, with a narrow sinus, the lobes broadly rounded, glabrous, green above and usually with a metallic luster, somewhat paler beneath and often purplish, the primary lateral nerves 4–5 on each side; peduncles 10–20 cm. long, 1 cm. thick, densely setose; spathe 7–11 cm. long, densely setose outside, greenish outside, purplish or whitish within, acute; spadix sessile, the pistillate portion pale, oblong, 4–5 cm. long or in fruit as much as 7 cm. and 2–3 cm. thick, the staminate portion whitish, 6–7 cm. long; pistils cylindric, 4- or 5-celled; berries whitish or pale yellowish, narrowly cylindric, almost 1 cm. long.

Dense, wet forest, usually at 1,000 meters or less but in Costa Rica ascending sometimes to 1,400 meters, Costa Rica to Colombia.

BOCAS DEL TORO: Old Bank Island, Chiriquí Lagoon, *Wedel* 1923; Tsaki, 200 m., *Tonduz* 9512 (fide Engler & Krause).

The leaves are handsome because of the deep, velvety green of the upper surface which often has a somewhat metallic sheen. Because of its handsome foliage, the species is sometimes cultivated in Europe, and probably also in hot-houses of the United States. Among all Central American Araceae it may be recognized at once by the densely setose petioles. Illustrated, *Pflanzenreich* IV. 23Db:75.

9. *PHILODENDRON WENDLANDII* Schott, Prodr. Aroid. 221. 1860.

A large or small, epiphytic vine, the caudex short or elongate, often 1 cm. or more in diameter, the internodes mostly elongate; petioles thick and succulent, 10–14 cm. long, semiterete; blades rather thick and subcoriaceous when dried, dark green, oblong or obovate-oblong, commonly 20–30 cm. long and 7–12 cm. wide but often larger, obtuse or rounded at the apex and cuspidate, shallowly cordate at the broad base, the sinus broad and open, often very shallow, the basal auricles broadly rounded, the primary nerves 7–10 on each side, widely spreading; peduncles short, stout, terete; spathes oblong-lanceolate, 14–18 cm. long, 5–7 cm. wide when expanded, white, short-acuminate, the tube equaling or slightly shorter than the limb; spadix subsessile, white, the pistillate portion cylindric, 4–5 cm. long, or in fruit to 7 cm. long and 1.5 cm. thick, the staminate part 6–8 cm. long, narrowed upward, very obtuse; pistils obovoid, 4- to 7-celled, capped by the small, orbicular stigma; berries red, subtetragonous-prismatic, 3 mm. long, 1.5 mm. thick; seeds ovoid, smooth, pale orange.

On trees in wet forest, lowlands of Panama and Costa Rica, at or near sea level.

CANAL ZONE: Río Indio de Gatún, *Pittier* 2794; Barro Colorado Island, *Aviles* 89; *Standley* 31308; *Shattuck* 851; hills north of Frijoles, *Standley* 27508; Balboa, cultivated, *Standley* 28542. COLÓN: Río Fató, *Pittier* 3867. BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *Wedel* 1479.

The local name is recorded as *Bejuco Desbinchador*. Illustrated, *Pflanzenreich* IV. 23Db: fig. 9.

10. *PHILODENDRON KARSTENIANUM* Schott, Syn. Aroid. 78. 1856.

A large or small, epiphytic vine, the caudex often 1 cm. or more in diameter, the internodes mostly 2-3 cm. long; petioles 10-20 cm. long, the sheath broad, green, persistent, rounded at the apex, ending 1 to several cm. below the base of the blade; blades thin when dried or somewhat coriaceous, narrowly elliptic-oblong to oblong-ovate, 15-30 cm. long, 7-13 cm. wide, rounded or obtuse at the apex and obliquely cuspidate, broadly rounded to short-cuneate at the base, the primary lateral nerves 7-8 on each side, divergent at a rather wide angle, all very slender or a few slightly more conspicuous than the others; peduncles 2-6 cm. long; spathes green, 6-14 cm. long, the tube ovoid or narrower, the limb whitish within, cuspidate, slightly shorter than the tube; spadix cylindric, borne on a stipe 5-8 mm. long, the pistillate portion 2-5 cm. long, the staminate 3-5 cm. long; pistils ovoid, 3- or 6-celled, crowned by the broadly discoid stigma, the ovules mostly 6-seriate; staminate flowers pale yellow, the stamens usually 3.

On trees in wet forest, usually near sea level, Panama to Venezuela and Ecuador.

CANAL ZONE: between Gorgona and Gatún, *Pittier 2262*; Gamboa, *Standley 28418*; near Gatún, *Standley 27224*; Barro Colorado Island, *Standley 31456, 40889*; *Wetmore & Woodworth II*.

Illustrated, Pflanzenreich IV. 23Db: fig. 3, H-P.

11. *PHILODENDRON COERULESCENS* Engler, Bot. Jahrb. 26:523. 1899.

Usually a large, scandent epiphyte, the caudex often greatly elongate, branched, the internodes 3-4 cm. long or more, rather stout and up to 1.5 cm. or more in diameter; petioles 12-20 cm. long, the sheath green, usually narrow and often deciduous, extending nearly or quite to the base of the blade; blades commonly thick when dried, broadly ovate or elliptic-ovate, mostly 25-35 cm. long and 15-20 cm. wide, obliquely cuspidate-acuminate, truncate or broadly rounded at the base or almost subcordate, the primary lateral nerves 15-16 on each side, divergent at a wide, often almost right angle, conspicuously stouter and more prominent than the secondary ones, 1.5-2 cm. apart; peduncles short and stout; spathes green or whitish, 12-18 cm. long, cuspidate; spadix subsessile, pale, the pistillate portion cylindric, 2.5-4 cm. long, 1.5-2 cm. thick, the staminate elongate-cylindric, 8-10 cm. long, 1 cm. thick, obtuse; pistils elongate-cylindric, truncate, 2 mm. long, capped by the concave, orbicular stigma, 4- or 5-celled, the ovules numerous; stamens 3-4.

Panama and Colombia, climbing over trees in wet forest, at or near sea level.

CANAL ZONE: Balboa, *Standley 25609*; Barro Colorado Island, *Standley 31258, 41138*; *Kenoyer 180*; *Wetmore & Woodworth 17*; *Frost 238*; Rio Chinilla, *Maxon 6891*; Mount Hope Cemetery, *Standley 28792*; Rio Chagres above Alhajuela, *Pittier 3504*; Obispo, *Standley 31707*.

12. *PHILODENDRON GUTTIFERUM* Kunth, Enum. Pl. 3:51. 1841.

Philodendron rigidifolium Krause, Pflanzenreich IV. 23Db:7, fig. 1, G-M. 1913.

Philodendron calderense Krause, Pflanzenreich IV. 23Db:8. 1913.

A large or small, epiphytic vine, the caudex stout, often 1 cm. in diameter,

the internodes 1–2.5 cm. long, or the lower ones longer; petioles stout and succulent, 5–14 cm. long, the sheath broad, green, rounded at the apex, extending to the base of the blade, usually persistent; blades thinly coriaceous when dried, elliptic-oblong to broadly oblong or rounded-ovate, mostly 10–18 cm. long and 6–12 cm. wide, obtuse to rounded at the apex and abruptly cuspidate or cuspidate-acuminate, broadly rounded to subacute at the base, the primary lateral nerves

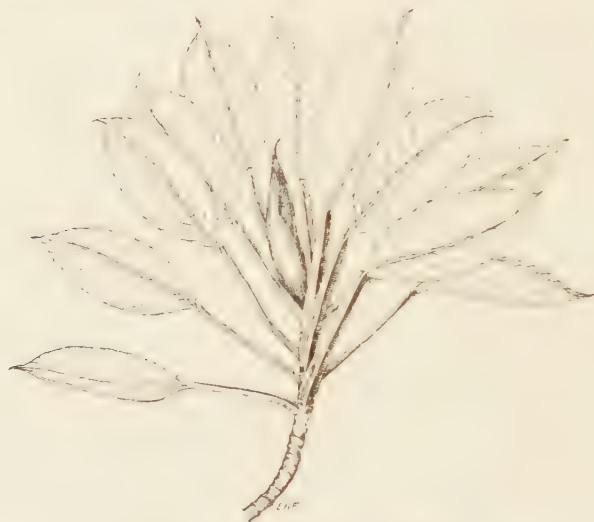


Fig. 91. *Philodendron guttiferum*

8–10 on each side, usually divergent at a wide angle but sometimes very oblique, scarcely stouter or more conspicuous than the secondary and tertiary ones; peduncles stout, 1–3 cm. long; spathes oblong, greenish or yellowish green, often cream-colored or white, 8–19 cm. long, the tube elongate, oblong, the limb open at anthesis, short-acuminate, coriaceous when dried; spadix sessile, cream-colored, cylindric, 10–16 cm. long, the pistillate portion about one-third as long as the staminate, the latter attenuate upward; pistils narrowly oblong, 4-celled, the ovules mostly 4-seriate; stamens 3–4.

On trees in wet forest, usually near sea level, Honduras to Panama and French Guiana.

CANAL ZONE: Barro Colorado Island, *Standley 40961*; *Wetmore & Woodworth 22*; hills north of Frijoles, *Standley 27477, 27545*; near Gatún, *Standley 27214*. COLÓN: Río Sirrí, Trinidad Basin, *Pittier 4013* (TYPE of *P. rigidifolium*). CHIRIQUÍ: forests around El Boquete, 1000–1300 m., *Pittier 3150* (TYPE of *P. calderense*); *Davidson 685*. BOCAS DEL TORO: Western River, Chiriquí Lagoon, *Wedel 2698*; Old Bank Island, Chiriquí Lagoon, *Wedel 1946*.

The name *Cinchadora* is said to be given in the Zone to this plant. After careful survey of the rather ample Central American material of this group now available for study, and after consideration of the characters upon which Krause's

two Panama species were based, it seems best to consider the three names cited as representing a single species, which also has as synonyms probably a number of other species considered distinct by Engler and Krause. Illustrated, Pflanzenreich IV. 23Db: fig. 3, A-G.

16. MONTRICHARDIA Crueger

MONTRICHARDIA Crueger, Bot. Zeit. 12:25. 1854.

Plants somewhat arborescent, the caudex erect, often very thick and solid, simple or sparsely branched, frequently supported by prop roots, sometimes covered with small prickles, leafy above; petioles vaginate to the middle or higher, clasping at the base, the sheath produced at the apex into a ligule; blades sagittate, the basal lobes shorter or longer than the anterior one, the primary nerves united to form a collective nerve close to the margin; peduncles usually solitary, shorter than the leaves; spathe large and thick, convolute below, open above, finally deciduous; spadix slightly shorter than the spathe, the pistillate portion cylindric, densely many-flowered, short, the staminate portion contiguous to the pistillate, very densely many-flowered; flowers monoecious, naked; staminate flowers with 3-6 stamens, these distinct, obpyramidal-prismatic, contiguous, truncate at the apex, the filaments obsolete; anthers subsessile, 2-celled, the cells oblong, acutish, dehiscent by a short apical slit; pistil of the pistillate flower subprismatic-obovoid, sessile, 1-celled; ovules 1-2, ascending, anatropous; style not sharply differentiated

from the ovary, the stigma sessile, orbicular; fruit large, baccate, spongy, excavate at the apex and radiately costate, 1-celled and 1-seeded; seed obovoid, the testa smooth, brown; endosperm none.

Two species are known, the other in Bahia, Brazil.

1. MONTRICHARDIA ARBORESCENS (L.) Schott,
Arac. Betreff. 1:4. 1854.

Arum arborescens L. Sp. Pl. ed. 2. 371. 1763.

Montrichardia Fendleri Schott, Gen. Aroid. pl. 49.
1858.

Caudex usually 1-3 m. high and supported at the base by prop roots, 1.5-2 cm. thick or at the base much thicker, green, the internodes chiefly short and only 1 cm. long, often armed with recurved prickles 2-3 mm. long; petioles 20-30 cm. long or more, terete above, the sheath extending above the middle; blades 15-40 cm. long or more, deeply sagittate, the basal lobes retrorse, acuminate to subobtus,



Fig. 92. *Montrichardia arborescens*

the anterior lobe triangular-ovate, broad, often cuspidate, the primary costal nerves 3-4 on each side; peduncle half as long as the spathe; spathes oblong-ovate, cuspidate, 10-15 cm. long and 6-7 cm. wide or larger, greenish or pale outside, white or whitish within; spadix very thick, the staminate portion 7 cm. long, the pistillate one-third as long; stamens 3-6; berries subglobose, 1-1.5 cm. in diameter.

In wet soil, most often in mud along the borders of tidal swamps or streams, British Honduras and Guatemala to Lesser Antilles and the Guianas.

CANAL ZONE and COLÓN: common in swamps of the Atlantic coast, and doubtless distributed along the whole coast.

Because of its peculiar habitat and characteristic leaf form, this plant is easy of recognition among other Panama aroids. The large, white spathes are conspicuous, and somewhat suggest those of the cultivated calla (*Zantedeschia*). Illustrated, Standl. Fl. Pan. Canal Zone, pl. 9; Engler, Pflanzenreich IV. 23C:123. *Montrichardia Fendleri* was based on *Fendler* 432 and 433 from Chagres.

LEMNACEAE

Plants very small or minute, oval, globular, or ensiform fronds (modified stems) free or variously attached, floating upon or beneath the surface of pools or sluggish streams, occasionally deposited on mud or wet rocks bordering a body of water. Roots present or absent. Inflorescence an extremely reduced spadix consisting of 1 pistillate and 1-2 staminate flowers, the whole immersed within a small pouch in the upper surface of the frond, naked or surrounded by an inconspicuous, vaginate spathe. Pistillate flowers naked, consisting of a single pistil containing 1 to several ovules. Staminate flowers naked, consisting of a single stamen.

The Lemnaceae include the Duck-weeds of the United States. They frequently occur in such great numbers that the whole surface of a pond may appear green, as though covered by a "water-bloom" of algae. For the determination of the Panamanian specimens cited in this account, the authors are indebted to Dr. W. H. Camp of the New York Botanical Garden. The text of the account is drawn largely from the works of C. H. Thompson (Ann. Rept. Missouri Bot. Gard. 7:101-111, pl. 64-66. 1896; *ibid.*, 9:21-42, pl. 1-4. 1898 [reprint, pp. 1-22. 1897]).

- | | |
|---|---------------|
| a. Fronds with solitary roots and 2 reproductive pouches..... | 1. LEMNA |
| aa. Fronds without roots and with 1 reproductive pouch. | |
| b. Fronds thin, ligulate..... | 2. WOLFFIELLA |
| bb. Fronds thick, globular | 3. WOLFFIA |

1. LEMNA L.

LEMNA L. Sp. Pl. 970. 1753; C. H. Thompson, Ann. Rept. Missouri Bot. Gard. 9:29. 1898 (reprint, p. 9. 1897).

Fronds attached by the basal margins, each bearing a solitary root; reproductive

pouches opening as clefts in either margin of the basal portion of the frond. Spadix of 1 pistillate and 2 staminate flowers, surrounded by an inconspicuous spathe.

- a. Fronds thin, without papillae along the midrib; root-cap strongly curved, gradually tapering to a narrow rounded tip..... 1. *L. CYCLOSTASA*
 aa. Fronds thicker, with a row of papillae along the midrib; root-cap slightly curved, cylindrical, with a bluntly rounded tip..... 2. *L. MINIMA*

1. *LEMNA CYCLOSTASA* (Ell.) Chev. Fl. Par. 2:256. 1827; Thompson, Ann. Rept. Missouri Bot. Gard. 9:35. 1898 (reprint, p. 15. 1897).

Lemna minor var.? *Cyclostasa* Ell. Sketch Bot. S. Car. & Ga. 2:518. 1824.

Lemna Valdiviana Phil. Linnaea 33:239. 1864.

Lemna Torreyi Aust. in Gray, Man. 479. 1867.

Lemna abbreviata Hgln. in Engl. Bot. Jahrb. 21:298. 1895.

Fronds solitary, or 2–8 attached in a more or less curved chain, oblong to obovate-oblong, usually somewhat falcate, 2.3–4.5 mm. long, 0.7–1.5 mm. broad, the base usually strongly asymmetrical, tapering into a short stipe or frequently sessile. Roots long, the cap strongly curved, tapering gradually to a small rounded tip.

Throughout the United States, southward into South America.

CHIRIQUÍ: rocky slopes of waterfall, Quebrada Velo, Woodson & Schery 240; in ditches, El Boquete, Pittier 3046. PANAMÁ: small pool, Juan Diaz, Standley 30547.

2. *LEMNA MINIMA* Phil. Linnaea 33:239. 1864; Thompson, Ann. Rept. Missouri Bot. Gard. 9:36. 1898 (reprint, p. 16. 1897).

Lemna platyclados Hgln. in Engl. Bot. Jahrb. 21:298. 1895.

Fronds solitary or adhering in groups of 2–4, oblong to elliptic, 3.9–1.5 mm. long, 0.9–2.7 mm. broad, bearing a row of minute papillae along the midrib. Roots slender, the cap slightly curved or straight, cylindrical, with a bluntly rounded tip.

Southern and western United States to South America.

CHIRIQUÍ: overflow of spring, Río Chiriquí Viejo valley, Seibert 179.

2. *WOLFFIELLA* Hgln.

WOLFFIELLA Hgln. in Engl. Bot. Jahrb. 21:303. 1895; Thompson, Ann. Rept. Missouri Bot. Gard. 9:37. 1898 (reprint, p. 17. 1897).

Fronds thin, ligular or ensiform, solitary or more frequently forming densely interwoven masses, without roots. Flowers and fruit unknown.

1. *WOLFFIELLA LINGULATA* Hgln. in Engl. Bot. Jahrb. 21:303. 1895; Thompson, Ann. Rept. Missouri Bot. Gard. 9:39. 1898 (reprint, p. 19. 1897).

Wolffia lingulata Hgln. Monogr. Lemnac. 132. 1868.

Fronds solitary or rarely in pairs, ovate to oblong-ligulate, slightly asymmetrical, 2.7–6.6 mm. long, 1.7–3.0 mm. broad.

Southern California, Mexico, Panama.

CANAL ZONE: Río Chagres, A. G. B. Fairchild 2099.

3. WOLFFIA Hork.

WOLFFIA Horkel ex Schleid. Linnaea 13:389. 1839; Thompson, Ann. Rept. Missouri Bot. Gard. 9:39. 1898 (reprint, p. 19. 1897).

Fronds minute, thick, globular, without roots. Spadix of 1 staminate and 1 pistillate flower, bursting through the tissues of the upper surface of the frond, without a spathe.

1. WOLFFIA PAPULIFERA Thompson, Ann. Rept. Missouri Bot. Gard. 9:40. 1898 (reprint, p. 20. 1897).

Fronds slightly asymmetrical under magnification, obliquely ovoid, more or less flattened above, gibbous beneath, brown-punctate, 1.0–1.5 mm. long, about 1 mm. broad.

Central United States, Mexico, Panama.

CANAL ZONE: Río Chagres, A. G. B. Fairchild 2099a.

Dr. Camp writes of this specimen: "Incidentally, in Fairchild 2099 [*Wolffiella lingulata*, vide supra] I found a single partly decomposed and much defunct specimen of what would seem to be *Wolffia papulifera* Thomps. I've been expecting this to bob up in Central America. I've seen it from Yucatan and collected it myself in Oaxaca. It's also abundant in certain areas in Michigan, S. Ohio and Kentucky. On your next trip try for a good collection to authenticate the species."

MAYACACEAE

1. MAYACA Aubl.

MAYACA Aubl. Hist. Pl. Guian. Fr. 1:42. 1775; A. C. Smith, N. Am. Fl. 19:1. 1937.

Slender moss-like herbs, the stems submerged or floating in fresh water, also growing in swamps. Leaves spiral, narrow, 1-nerved, minutely emarginate, sessile. Flowers perfect, axillary, solitary or in clusters, the pedicels slender, bracteate. Sepals 3, equal. Petals 3, equal. Stamens 3, hypogynous, alternate with the petals; filaments free, somewhat dilated at the base; anthers basifixed, 4-celled, dehiscing by a single apical or subapical pore. Ovary superior, 1-celled; ovules several on 3 parietal placentae. Fruit a 3-gonal, septicidal capsule.

a. Stems usually tufted or matted; pedicels usually longer than the leaves; capsule subglobose or ovoid, nearly as broad as long..... 1. M. AUBLETI

aa. Stems usually weak and elongate; pedicels usually shorter than the leaves; capsules oblong-ellipsoid, nearly twice as long as broad..... 2. M. FLUVIATILIS

1. MAYACA AUBLETI Michx. Fl. Bor. Am. 1:26. 1803; A. C. Smith, N. Am. Fl. 19:2. 1937.

Syena Nuttalliana Schultes in R. & S. Syst. 1:343. 1822.

Mayaca Michauxii Schott & Endl. Melet. 24. 1832.

Syena Aubleti Michx. in Schott & Endl. loc. cit. 1832, in synonym.
Mayaca longipes Gandoger, Bull. Soc. Bot. Fr. 66:293. 1920.

Stems usually tufted or matted, 2–20 cm. long. Leaves densely crowded, narrowly lanceolate to linear-lanceolate, 3–5 mm. long. Flowers violet to pink or white; pedicels 4–25 mm. long; sepals ovate-lanceolate, 3–4 mm. long; petals ovate, 3–4 mm. long, rounded at the tip. Capsules broadly ovoid, 2.5–4.5 mm. long.

Southern Virginia to Florida and Texas; Cuba, eastern Mexico to Panama.

PANAMÁ: Nuevo San Francisco, *Standley* 30773; Las Sabanas, *Standley* 40772; Chepo, *Pittier* 4678.



Fig. 93. *Mayaca fluviatilis*

2. *MAYACA FLUVIATILIS* Aubl. Hist. Pl. Guian. Fr. 1:42. 1775; A. C. Smith, N. Am. Fl. 19:1. 1937.

Syena Mayaca J.F.Gmel. Syst. Nat. 2:121. 1791.
Syena fluviatilis (Aubl.) Willd. Sp. Pl. 1:254. 1797.

Mayaca Wrightii Griseb. Cat. Pl. Cub. 224. 1866.
Mayaca caroliniana Gandoger, Bull. Soc. Bot. Fr. 66:293. 1920.

Stems elongate and trailing, often submerged. Leaves very numerous, linear-lanceolate or filiform, 4–20 mm. long, 0.3–0.6 mm. broad. Flowers violet to pink or white; pedicels 1–5 mm. long; sepals ovate-lanceolate, 3–4 mm. long; petals ovate, 3–4 mm. long. Capsules oblong-ellipsoid, 3.5–5.0 mm. long, 1.5–3.0 mm. broad.

North Carolina to Florida and Mississippi; Cuba, Jamaica, Hispaniola, Panama and northern South America, Trinidad. In swamps and temporary pools in savannas.

PANAMÁ: road to Chepo, *Hunter & Steyermark* s. n.

It is rather questionable whether these species represent distinct biological entities.

XYRIDACEAE

1. XYRIS L.

XYRIS L. Sp. Pl. 42. 1753; Malme, N. Am. Fl. 19:3. 1937.

Kotsjiletti Adans. Fam. Pl. 2:60, 544. 1763.

Perennial, occasionally annual, tufted herbs of damp or wet situations. Leaves mostly basal, linear, terete, or lanceolate, sheathing at the base. Flowering scapes erect, simple, terminated by a solitary dense spike or head, and usually bearing 1 to several bladeless sheaths at the base. Flowering spikes or heads globose to elongate; bracts glumaceous, rather rigid or thin and papery, spirally imbricated, the lower usually sterile, the upper subtending the rather inconspicuous flowers. Flowers perfect, solitary and sessile in the axils of the bracts, yellow or blue, rarely white. Sepals 2-3, unequal. Petals 3, usually equal, obovate-spatulate, the basal claws free or united. Stamens 3, opposite the petals and adnate to claws; filaments usually short and flattened; anthers basifixed, 2-celled, dehiscent longitudinally. Staminodes (when present) 3, alternating with the petals, usually bifid at the tip, the branches usually tipped with brush-like tufts of moniliform hairs. Ovary 1-celled or imperfectly 3-celled; ovules numerous; style filiform, usually 3-cleft at the tip. Capsule loculicidal.

1. *Xyris JUPICAI* L. C. Rich. Act. Soc. Hist. Nat. Paris 1:106. 1792; Malme, N. Am. Fl. 19:11. 1937.



Fig. 94. *Xyris Jupicai*

Xyris communis Kunth, Enum. 4:12. 1843.

Xyris surinamensis Miq. Linnaea 17:58. 1843.

Xyris arenicola Miq. ibid. 18:75. 1844.

Xyris acuminata Miq. ex Steud. Syn. Cyp. 284
1855.

Xyris gymnoptera Griseb. Cat. Pl. Cub. 223. 1866.

Somewhat tufted or annual. Leaves linear, 12-30 (-40) cm. long, acute, smooth or rarely minutely tuberculate beneath; sheath $\frac{1}{3}$ - $\frac{1}{2}$ the length of the blade. Flowering scapes slender, 1- to 2-costate, 3-6 dm. tall; spikes many-flowered, ovoid or ellipsoid, 8-13 mm. long, 5-8 mm. thick, the flowering bracts obovate, 5-7 mm. long, 3.5-4.5 mm. broad, entire, tawny or rusty, somewhat shining, bearing on the outer face a greenish ovate area about 2 mm. long. Sepals 2, included within the bracts, the keel entire below, lacerate-dentate from above the middle. Petals yellow, 5 mm. long.

Maryland to Florida and Texas, Mexico south to Uruguay; Greater Antilles. In wet savannas and marshes.

COCLÉ: Aguadulce, Pittier 4836.

ERIOCAULACEAE

BY HAROLD N. MOLDENKE

Perennial or rarely annual aquatic or marsh herbs, mostly short-stemmed, usually monoecious, rarely dioecious; roots tufted, fibrous, knotty or spongy, often septate; leaves mostly basal and tufted, grass-like, usually crowded, often pellucid and loosely cellular, sometimes membranous; inflorescence capitate, in terminal solitary or umbellately aggregate involucrate heads, borne on long slender often scapose peduncles, which are sheathed at base; florets mostly actinomorphic, numerous, small, sessile or short-pedicellate on a variously shaped receptacle, usually each borne in the axil of a scarious scale-like colored or colorless receptacular bractlet, unisexual, mostly androgynous, the staminate and pistillate mixed together or the staminate in the center and the pistillate on the periphery, the sexes very rarely in separate heads; perianth (perigonium) scarious (chaffy) or membranous, rarely hyaline, its segments 2- or 3-merous, usually in 2 distinct series, the outer (calyx) free or rarely partially connate, the inner (corolla) often united in an infundibular fashion, rarely absent; stamens as many as the outer perianth-segments and alternate with them, or twice as many, inserted on the corolla (when present); filaments distinct; anthers small, 2- or 4-celled, composed of 1 or 2 thecae, opening by longitudinal slits, introrse; staminodes rarely present in pistillate florets; ovary superior, 2- or 3-locular; style terminal, often appendaged; stigmas 2 or 3, simple or lobed; ovules solitary and pendulous in each locule, orthotropous; fruit a 2- or 3-celled, 2- or 3-seeded, membranous capsule, loculicidally dehiscent; seeds solitary, pendulous, with a small embryo borne at the apex of a copious mealy endosperm; cotyledon one.

- a. Stamens 4 or 6, twice as many as the outer perianth segments (rarely 3) 1. ERIOCAULON
 aa. Stamens 2 or 3, as many as the outer perianth segments.
 b. Anthers 4-celled, composed of 2 thecae; stems not floating.
 c. Inner perianth segments of pistillate florets free 2. PAEPALANTHUS
 cc. Inner perianth segments of pistillate florets connate at the middle ... 3. SYNGONANTHUS
 bb. Anthers 2-celled, composed of 1 theca; stems usually floating 4. TONINA

1. ERIOCAULON L.

ERIOCAULON L. Sp. Pl., ed. 1, 87. 1753; Gen. Pl., ed. 5, 38. 1754.

Cespa Hill, Herb. Brit. 1: pl. 66 (some copies). 1769.

Nasmythia Huds. Fl. Ang., ed. 2, 414. 1778.

Randalia Petiv. ex Desv., Ann. Sci. Nat. Paris I, 13:47, pl. 5, fig. 2. 1828.

Symphachne P. Beauv. ex Desv. op. cit. 47, pl. 5, fig. 3. 1828.

Sphaerochloa P. Beauv. ex Desv. op. cit. 47. 1828.

Sphaerochloa P. Beauv. op. cit. pl. 5, fig. 1. 1828.

Leucocephala Roxb. Fl. Ind. 3:612. 1832.

Electrosperma F. Muell. Trans. Phil. Soc. Victoria 1:23. 1855.

Dichrolepis Welw. Apont. Phyt.-geogr. 542. 1859.

Lasiolapis Böck. Flora 56:90. 1873.

Stems mostly very short, rarely elongate and equally covered with leaves throughout; leaves mostly tufted, membranous or very thin and pellucid, more or

less linear or linear-lanceolate and grass-like, sessile and clasping at the base, very often fenestrate; florets dimerous or trimerous, the staminate mixed with the pistillate or segregated on separate heads or (rarely) on separate plants; perigonium almost always double; staminate florets with the sepals free at the base or often more or less connate into a split spathe, the 2 or 3 petals united below into a tube, free at the apex, the lobes usually bearing a small black gland on the inner surface near the apex; stamens twice as many as the sepals (or rarely 3) and exserted; anthers 4-celled, mostly black, composed of 2 thecae; pistillate florets with free or (rarely) spathaceous-connate sepals; petals free or rarely none, usually each bearing a small black gland slightly below the apex within; style-appendages none; stigmas 2 or 3, simple.

- a. Both staminate and pistillate florets dimerous; stamens 4; stigmas 2; ovary 2-ovulate.
 - b. Heads dark gray; peduncles to 9.5 cm. long; receptacular and involucre bractlets light brown, sharply acute or acuminate at the apex. 1. *E. SEEMANNII*
 - bb. Heads lightly flavescent-stramineous; peduncles to 19.5 cm. long; receptacular and involucre bractlets hyaline or flavescent, broadly rounded at the apex. 2. *E. WOODSONIANUM*
- aa. Both staminate and pistillate florets trimerous; stigmas 3; ovary 3-ovulate.
 - b. Sepals of mature staminate florets not spathaceous; involucre bractlets fuscous-nigrescent, obovate or subrotund. 3. *E. PANAMENSE*
 - bb. Sepals of mature staminate florets connate into a split spathe; involucre bractlets light-stramineous, ovate. 4. *E. WILLIAMSONII*



Fig. 95. *Eriocaulon Seemannii*

1. *ERIOCAULON SEEMANNII* Moldenke, N. Am. Fl. 19:28. 1937.

Stems very short; leaves olivaceous, tufted, spreading or recurved, linear-lanceolate, 2.3–6 cm. long, 2.5–3 mm. wide at the middle, very thin-membranous or subpellucid, subulate-acute or acuminate at the apex (the tip itself bluntish), fenestrately 5- to 7-nerved (the fenestrations very conspicuous on both surfaces), glabrate; peduncles aggregate, very numerous, 19–40 per plant, slender, olivaceous, 4–9.5 cm. long, 3-costate, glabrous; sheaths loose, 1.5–4 cm. long, rather obscurely striate and fenestrate, bilobed at the apex, the blades short and sharply acute, scarious-margined; heads dark gray, hemispheric or globose, 2.5–4 mm. in diameter, slightly compressed in drying; involucre bractlets light brown, broad, elliptic, acute, glabrous; receptacle long-pilose; receptacular bractlets light brown (or hyaline at the base), spatulate, acute or acuminate, sparsely pubescent on the back; staminate florets: pedicellate; sepals 2, light brown toward

the apex, hyaline below, oblong or subobovate, concave, bluntish; petal-tube pale stramineous, its lobes very minute; anthers 4, black, roundish; pistillate florets: short-pedicellate; sepals 2, brown, spatulate, navicular, subacute, broadly winged-carinate at the middle, not crested, sparsely pilose at the apex; petals 2, pale stramineous, unequal, obovate, blunt, not notched, glabrous; ovary long-stalked, 2-ovulate; style shorter than the ovary; stigmas 2, longer than the ovary.

Wet meadows, Panama.

CANAL ZONE: meadows near Panamá City, *Seemann* 295. PANAMÁ: boggy grasslands and marginal thickets, between Pacora and Chepo, alt. about 25 m., *Woodson, Allen & Seibert* 1650; scarce in marsh, vicinity of Juan Franco race track, near Panamá, *Standley* 27821.

The Standley collection was originally distributed as *E. Schiedeianum* Körn., a trimerous Mexican species. *E. Seemannii* is thus far known only from Panama.

2. *ERIOCAULON WOODSONIANUM* Moldenke in Woodson & Schery, Ann. Missouri Bot. Gard. 27:268. 1940.

Dwarf plants; leaves tufted, erect or spreading, thin-membranous or pellucid, light green, linear, 4–7 cm. long, 1.5–3 mm. wide at the middle, subulate at the apex, not at all revolute along the margins, glabrous, fenestrately many-nerved (the fenestrations especially conspicuous beneath); peduncles 5–21 per plant, slender, 6.5–19.5 cm. long, 3-costate, slightly twisted, glabrous; sheaths loose, 3–5 cm. long, much shorter than the leaves, glabrous, not fenestrate, deeply lobed at the apex; heads hemispheric, lightly flavescent-stramineous, 3–4.5 mm. in diameter; involucre bractlets scarious, hyaline or stramineous, varying from ovate to elliptic or obovate, about 3 mm. long, 2–2.5 mm. wide, obtuse at the apex, usually not much narrowed at the base; receptacular bractlets broadly elliptic, scarious, somewhat flavescent along the midrib and at the apex, hyaline toward the margins, about 2.4 mm. long and wide, rounded at the apex, somewhat narrowed at the base, decidedly navicular and closely imbricate; staminate florets: pedicellate (pedicels about 0.5 mm. long); sepals 2, free to the base, obovate, about 1.5 mm. long and about equally wide at the apex, hyaline, transparent, conduplicate around the corolla-tube, carinate in a median line on the back, slightly emarginate at the apex, erect, glabrous throughout; corolla-lobes 2, minute, obtuse, non-glanduliferous; stamens 4; anthers brown; pistillate florets: pedicellate (pedicels about 0.5 mm. long); sepals 2, broadly obovate, hyaline, transparent, about 1.7 mm. long and equally wide at the apex, slightly emarginate, flat (not conduplicate), with a very broad wing or crest on the median keel on the back, glabrous; petals 2, free, hyaline, spatulate, transparent, about 1.9 mm. long, about 0.7 mm. wide at the apex; ovary 2-celled.

Known only from the type collection.

PANAMÁ: margin of pool in savanna along road between Panamá and Chepo, *Dodge, Hunter, Steyermark & Allen* 16717.

3. *ERIOCAULON PANAMENSE* Moldenke, N. Am. Fl. 19:31. 1937.

Stems very short; leaves tufted, erect, olivaceous, brunnescens in drying, broadly linear, 3.5–7.7 cm. long, about 3 mm. wide at the middle, very blunt, fenestrately many-nerved (the fenestrations plainly discernible, more conspicuous beneath and at the base), glabrate; peduncles aggregate, 3 or 4 per plant, slender, brunnescens, about 5-costate, slightly or not at all twisted, glabrous; sheaths loose, 4.5–6 cm. long, very obscurely fenestrate and striate, not twisted, obliquely split at the apex, the blade short and blunt, scarious-margined; heads hemispheric, 4–7 mm. in diameter, compressed in drying; involucreal bractlets fuscous-nigrescent, obovate (or the outermost subrotund), rounded at the apex, glabrous; receptacle glabrous; receptacular bractlets stramineous below, olivaceous-nigrescent toward the apex, obovate, acute, short-pilose toward the apex; staminate florets: sepals 3, connate at the very base only, nigrescent, plane or subnavicular, spatulate, obtuse, sparingly pilose on the back at the apex; petal-tube stramineous, its lobes 3, short, unequal, ciliate; stamens 6; anthers black, oblong; pistillate florets: sepals 3, nigrescent throughout, spatulate, navicular-concave, not alate, rounded to subacute at the apex, short-pilose on the back for the upper third and at the apex; petals 3, free, obovate, pale stramineous, black-glanduliferous at the apex, short-pilose within; style as long as the ovary; stigmas 3, twice as long as the style; ovary 3-celled.

Known only from the type locality.

CHIRIQUÍ: wet meadows along Río Caldera, south of El Boquete, alt. 1250–1500 m., *Killip* 3614; swampy meadows, Finca Lérída to Boquete, alt. 1300–1700 m., *Woodson, Allen & Seibert* 1130.

4. *ERIOCAULON WILLIAMSHII* Moldenke, N. Am. Fl. 19:36. 1937.

Dwarf plants; leaves tufted, erect or spreading, thin-membranous or pellucid, light green, linear, 1–4.5 cm. long, 1–2 mm. wide at the middle, subulate at the apex, often slightly revolute on old leaves, fenestrately many-nerved (the fenestrations especially conspicuous beneath), glabrous; peduncles 3 or 4 per plant, slender, 1.2–6.5 (–10) cm. long, usually rather obscurely 3-costate or striate, subglabrate; heads hemispheric or ovate-conic, dark gray, 2.5–4 mm. in diameter, compressed in drying; involucreal bractlets rather few, light stramineous, ovate, blunt, glabrous; receptacle glabrous; receptacular bractlets hyaline, with a grayish median line at the middle on the back, obovate, acute, glabrous; staminate florets: long-pedicellate; sepals 3, nigrescent, spathaceous, the lobes short, often incurved and acute, glabrous; petal-tube pale stramineous, its lobes very minute, glabrous; anthers 6, white, rotund; pistillate florets: pedicellate; sepals 3, hyaline (or grayish toward the apex), narrowly linear, glabrous; petals hyaline, narrowly linear, glabrous; style elongate, longer than the long-stalked ovary; stigmas 3, longer than the ovary.

British Honduras and Panama.

COCLÉ: on clay of dried-up pond at Penonomé and vicinity, alt. 15–300 m., *Williams* 299.

2. PAEPALANTHUS Mart.

PAEPALANTHUS Mart. Nov. Act. Phys.-med. Acad. Caes. Leopold.-Carol. Nat. Cur. 17¹:13. 1835. *Nomen conservandum*.

Dupatya Vell. Fl. Flum. 35. 1825. *Nomen rejiciendum*.

Stephanophyllum Guill. in Deless. Icon. Sel. 3:61, pl. 98. 1837, in obs.

Cladocaulon G. Gardn. in Hook. Icon. Pl. pl. 528. 1843.

Limnoxeranthemum Salzm. ex Steud. Syn. Pl. Cyp. 2:281. 1855, in syn.

Stems and branches very variable; leaves thin-membranous to thick-coriaceous, usually not fenestrate; heads villous; receptacular bractlets present; florets mostly polygamous, 2- or 3-merous; perianth (perigonium) double and involute; staminate florets with the sepals more or less connate toward the base, the petals connate into a membranous, hollow, glabrous (or rarely pilose within), slightly 2- or 3-lobed, eglandular, infundibular tube, which is finally almost always involute; stamens of the same number as the petals (2 or 3) and opposite them, exserted; anthers 4-celled (composed of 2 thecae); and in the center a double or triple papillose rudimentary pistil; pistillate florets with the sepals usually connate at the very base and becoming rigid in age; petals free and eglandular; ovary 2- or 3-celled, the style-appendages mostly 2 or 3, papillose at the apex, inserted at about the same height as the stigmas and placed between them; the stigma simple or more often bifid; hairs of the receptacular bractlets and perigonium granulose within, almost always clavate-obtuse, often tuberculate.

1. PAEPALANTHUS LAMARCKII Kunth, Enum. Pl. 3:506. 1841.

Eriocaulon fasciculatum Lam. Encycl. Méth. 3:276. 1789 (not *E. fasciculatum* Rottb., 1778).

Paepalanthus Ottonis Klotzsch in Schomb. Reise in Br. Guian. 3:1115. 1848.

Eriocaulon Lamarckii (Kunth) Steud. Syn. Pl. Cyp. 276. 1855.

Lasiolipsis pilosa Bock. Flora 56:90. 1873.

Dupatya Lamarckii (Kunth) Kuntze, Rev. Gen. Pl. 2:746. 1891.

Stems simple, 2-8 cm. long; leaves dull- or grayish-green, the older ones olivaceous, plane, linear-lanceolate or broadly linear, 1.3-3 cm. long, 0.5-2.3 mm. wide at the middle, amplexate-clasping at the base, narrowed to a rather acute or obtuse apex, many-striate, sparsely puberulent or pilose, soon glabrescent; peduncles fasciculate at the apex of the stem, 2-20 per plant, usually numerous, 1.5-7 cm. long, irregularly and more or less densely spreading-pilose; sheaths rather loose, 9-13 mm. long, long-pilose, the blade rather rigid, often lobed or bifid, attenuate and sharply acute at the apex, often somewhat spreading, long-ciliate, at first puberulent, eventually calvescent; heads dark brown, globose, 2-3 mm. in diameter, villous; involucre bractlets gray-brown, with a lighter midrib, obovate, subacute and densely pilose at the apex; receptacle pilose; receptacular bractlets brown, with a white midrib, spatulate, acute at the apex, densely long-pilose above the middle on the back; staminate florets: sepals 3, stramineous at the base, dark brown at the apex (except for a broad white central band), spatulate, obtuse and

ciliate at the apex; petal-tube stramineous; stamens 3; pistillate florets: sepals similar in color and texture to those of the staminate florets, obovate, pilose along the margins and at the apex, spreading; petals 3, tiny, white or hyaline, linear, blunt and sparsely ciliate at the apex; ovary 3-celled; style-appendages long and hyaline; stigmas 3, brown, shorter than the style-appendages; seeds slightly curved, cancellate.

Hispaniola, Cuba, and British Honduras to Panama, Trinidad, and Brazil.

COCLÉ: in savannas near sea-level, Aguadulce, *Pittier 4932*; marshy places, lower portion of valley and marshes along Río Antón, El Valle de Antón, alt. about 500 m., *Hunter & Allen 365*.

3. SYNGONANTHUS Ruhl.

SYNGONANTHUS Ruhl. in Urb. Symb. Ant. 1:487. 1900.

Stems very short or elongate, sterile or fertile, simple or branched; roots rather thick or incrassate, porous, whitish; heads pilose or subglabrate, the hairs always acute and smooth; receptacular bractlets almost always none; florets trimerous; sepals mostly free or almost so; staminate florets with the petals connate into an infundibular, 3-lobed, glabrous, finally almost always involute (rarely 3-parted) tube and the anthers 4-celled, composed of 2 thecae; pistillate florets with the petals connate by their margins at or above the middle, the base and apex free, the apex finally mostly involute; style terete, its appendages non-papillose, sometimes obsolete; stigmas simple, inserted at the same height on the style as its appendages.

1. SYNGONANTHUS PITTIERI Moldenke in Woodson & Schery, Ann. Missouri Bot. Gard. 27:269. 1940.

Dwarf plants; leaves few, tufted, recurved and usually closely appressed to the ground, membranous, olivaceous, linear, 1–1.5 cm. long, to 1 mm. wide at the middle, attenuate and subulate at the apex, densely strigose with whitish appressed antrorse hairs on both surfaces, not fenestrate; sheaths tightly appressed, 2–2.5 cm. long, greatly surpassing the leaves, densely pilose with irregular whitish hairs, deeply lobed at the apex; peduncles several per plant, stramineous, slender, rather obscurely costate, slightly twisted, glabrous; heads hemispheric, light gray or ashy, 3.5–4.5 mm. wide; involueral bractlets membranous, narrowly obovate or oblanceolate, about 2 mm. long and 1 mm. wide, brunnescent toward the middle, hyaline at the margins; receptacular bractlets none; staminate florets: pedicellate; pedicels about 0.5 mm. long, villous; sepals hyaline, transparent, narrow-elliptic, about 1.2 mm. long, about 0.5 mm. wide, glabrous; petal-tube hyaline, translucent, about 1.5 mm. long, 3-lobed at the apex; anthers 3, white; pistillate florets: pedicellate (pedicels about 0.7 mm. long, villous); sepals 3, free, hyaline, transparent, narrowly lanceolate, about 1.7 mm. long, about 0.5 mm. wide at the base, sharply acute or acuminate at the apex, glabrous throughout; petals narrowly oblong, hyaline and transparent, about 1 mm. long and 0.3 mm. wide, glabrous, connate by their margins above, free at the base.

Known only from the type collection.

CHIRIQUÍ: Sabana de El Boquete, alt. 700–1100 m., Pittier 3316.

4. TONINA Aubl.

TONINA Aubl. Hist. Pl. Guian. Fr. 2:856. 1775.

Hyphydra Schreb. Gen. 666. 1791.

Stems elongate, slender, usually floating, equally foliose throughout; peduncles apparently supra-axillary; florets trimerous, pedicellate; receptacle pilose; staminate florets with the sepals connate to the middle, the 3 petals connate into a short membranous shortly 3-lobed tube, which is concave above, 3 stamens, and 2-celled anthers (composed of 1 theca); pistillate florets with 3 rather thick and somewhat porous sepals, which are connate at the base, very small free long-pilose petals, 3 non-papillose style-appendages, and 3 bifid stigmas which are shorter than the style-appendages.

1. TONINA FLUVIATILIS Aubl. Hist. Pl. Guian. Fr. 2:857, *pl.* 330. 1775.

Hyphydra amplexicaulis Vahl, Symb. Bot. 3:99. 1794; Schreb. apud Ruhl. in Engl. Pflanzenreich 4⁸⁰:240. 1903, in syn.

Eriocaulon amplexicaule (Vahl) Rottb. Descr. Pl. Surinam. 7, *pl.* 1, *fig.* 1. 1798.

Stems greatly elongate, slender, lax, 20–80 or more cm. long, often branched, about 1 mm. in diameter, equally and persistently foliose; leaves rather dense, spreading, lanceolate or oblong, 0.8–1.5 cm. long, 1–2.5 mm. wide at the middle, sessile and more or less clasping at base, acute and often recurved at apex, long-ciliate along the margins throughout or sparsely ciliate at base only and otherwise glabrous on both surfaces; peduncles dispersed over the stem and branches, 2–13 mm. long (mostly about 1 cm. long when mature), glabrous; heads echinulate-globose, 4–8 mm. in diameter, subglabrate; involucre bractlets ovate or obovate, long-cuspidate, glabrous except for the pilose-ciliate base and apex, the outer ones broader; receptacular bractlets narrowly oblong-obovate, cuspidate-acuminate, ciliate below the apex; staminate florets: sepals 3, fuscous, broadly obovate, connate to the middle, involute above, abruptly acute at apex, very concave ventrally; pistillate florets: sepals ovate, concave ventrally, long-cuspidate, ciliate; petals linear.

Quiet water of marshes, swamps, ponds, and streams from Cuba and British Honduras to Colombia, Trinidad, and Brazil.

CHIRIQUÍ: Río Caldera, Boquete, Woodson & Schery 752.

RAPATEACEAE

1. STEGOLEPIS

STEGOLEPIS Klotzsch ex Koernicke, Linnaea 37:480, *pl.* 1, *fig.* 22–25. 1872; Pilger in Engl. & Prantl, Nat. Pflanzenfam. 15a:63. 1930.

Rather massive epiphytic or marsh herbs somewhat resembling large sedges.

Stem a fleshy naked rhizome. Leaves equitant, relatively large, broadly sheathing at the base, the elongate blade orientated at approximately 180° to the sheath. Flowering scapes axillary, elongate, very slender, naked, bearing 1 to few sessile 1-flowered heads at the tip. Flower heads sheathed at the base by several pairs of small subscarios bracts. Sepals 3, equal, coherent at the base. Petals 3, equal, coherent at the base into a tube. Stamens 6, epipetalous, equal; filaments rather short; anthers basifixed, dehiscent by an apical pore. Pistil 3-celled, multi-ovulate. Fruit a loculicidal capsule.



Fig. 96. *Stegolepis Allenii*

COCLÉ: El Valle de Antón, Allen 2153.

1. *STEGOLEPIS ALLENII* Steyermark in Standl. & Steyerm. Field Mus. Bot. Ser. 22:325. 1940.

Epiphytic acaulescent herbs from a thick elongate rhizome about 10 cm. long and 1.5 cm. thick. Leaves distichous, ensiform, 30–40 cm. long, 1.5–2.8 cm. broad, acute, narrowed toward the basal sheath; sheath triangular-ovate, 10–15 cm. long, 2.5–3.5 cm. broad. Flowering scapes very slender, 30–50 cm. long, gradually dilating to the 1–2 sessile flowering heads. Flowering heads narrowly elliptic, about 1 cm. long, sheathed at the base by several pairs of closely imbricated ovate to ovate-lanceolate bracts 1–7 mm. long, glabrous.

Panama, epiphytic in highland forest.

BROMELIACEAE

By LYMAN B. SMITH

Herbs in all the Panamanian species, mostly epiphytic or saxicolous. Leaves spirally arranged, usually basal, simple, entire or spinose-serrate, at least in youth bearing peltate scales serving to collect and hold moisture. Inflorescence simple or compound, usually bearing brightly colored bracts. Flowers perfect or functionally dioecious. Perianth heterochlamydeous with 3 sepals and 3 petals, the segments of each series free or variously joined. Stamens 6, the filaments free or joined to the petals or to each other. Ovary superior to inferior, 3-celled. Fruit capsular or baccate. Seeds naked, winged or plumose. Embryo small, at the base of the mealy endosperm. About 50 genera and 1,500 species, indigenous to tropical and subtropical America except for a single African species.

- a. Ovary wholly or partly superior; fruit capsular; seeds appendaged.
 - b. Seeds with entire appendages; leaves of the Panamanian species spinose-serrate; ovary only in part superior; plants usually terrestrial..... 1. PITCAIRNIA
 - bb. Seeds plumose; leaves always entire; ovary nearly or quite superior; plants chiefly epiphytic.
 - c. Appendage of the seed basal, straight at maturity (for key to fruiting specimens of genera 2-5 see p. 79).
 - d. Petals nearly or quite free.
 - e. Petals naked; inflorescence of one or more distichous-flowered spikes or rarely simple and polystichous..... 2. TILLANDSIA
 - ee. Petals each bearing 2 scales on the inner surface.
 - f. Inflorescence of one or more distichous-flowered spikes; floral bracts usually forming the conspicuous element of the inflorescence; branches usually elongate when present..... 3. VRIESIA
 - ff. Inflorescence of several polystichous-flowered spikes, though the flowers sometimes turning secund or the spikes reduced to single flowers (but the two series of bracts indicating a compound inflorescence); primary bracts the conspicuous element of the inflorescence; branches usually short..... 4. THECOPHYLLUM
 - dd. Petals joined or closely agglutinated for most of their length; inflorescence always of polystichous-flowered spikes..... 5. GUZMANIA
 - cc. Appendage of the seed apical, folded over at maturity; sepals distinctly asymmetric in all Panamanian species; flowers polystichous..... 6. CATOPSIS
- aa. Ovary inferior; fruit baccate; seeds naked; leaves mostly serrate.
 - b. Ovaries remaining distinct; inflorescence without a large foliaceous coma.
 - c. Petals joined to the filament-tube but with free margins, fleshy, 3-4 cm. long; sepals with soft points; flowers pedicellate; inflorescence compound..... 7. BROMELIA
 - cc. Petals free, not fleshy; filaments not forming a tube.
 - d. Petals up to 43 mm. long, spirally recurved at anthesis, linear; sepals unarmed, symmetric; inflorescence simple, pendulous..... 8. BILLBERGIA
 - dd. Petals erect or divergent at anthesis; sepals mostly pungent or mucronate, usually asymmetric; petals usually small..... 9. AECHMEA
 - bb. Ovaries fusing into a syncarp; inflorescence bearing a large foliaceous coma..... 10. ANANAS

1. PITCAIRNIA L'Hérit.

PITCAIRNIA L'Hérit. Sert. Angl. 7. 1788. *Nomen conservandum*.

Hepetis Sw. Prodr. 4, 56. 1788.

Conanthes Raf. Fl. Tell. 4:24. 1838.

Neumannia Brongn. Ann. Sci. Nat. II. 15:369. 1841.

Lamproconus Lemaire, Jard. Fleur. 2:pl. 127. 1852.

Cochliopetalum Beer in Flora 37:347. 1854.

Phlomostachys Beer, Bromel. 16, 45. 1857.

Orthobopetalum Beer, Bromel. 17, 70. 1857.

Pepinia Brongn. ex André, Ill. Hortic. 17:32. 1870.

Melinonia Brongn. ex E. Morr. Cat. Bromél. Liège, 10. 1873.

Plants mostly terrestrial, rarely epiphytic, usually stemless. Leaves fasciculate or imbricate along a stem, entire or spinose-serrate, the sheath small, often bulbous-thickened, the blades linear to lanceolate with a definite petiole or narrowly triangular, sometimes dimorphic with some blades reduced to horny spinose-serrate spines, the larger blades sometimes deciduous. Inflorescence simple or compound. Flowers perfect, pedicellate to subsessile. Sepals free, acute or obtuse. Petals free, slightly zygomorphic in most species, naked or appendaged on the inside near base. Stamens from shorter to longer than the petals, the anthers linear. Ovary usually superior for most of its length. Style filiform. Ovules many, usually caudate. Capsule usually septicidal. Seeds caudate at both ends or rarely with an annular wing.

- a. Floral bracts exceeding the sepals, broad.
 - b. Leaf-blades petiolate, 55–125 mm. wide; inflorescence cylindric, elongate.
 - c. Sepals oblong, 25 mm. long; flowers remaining erect; leaves 55–60 mm. wide..... 1. *P. ATRORUBENS*
 - cc. Sepals oblanceolate, 45 mm. long; flowers often spreading at anthesis; leaves 105–125 mm. wide..... 2. *P. OBLANCEOLATA*
 - bb. Leaf blades sessile, linear, 5–7 mm. wide..... 3. *P. APHELANDRAEFLORA*
- aa. Floral bracts shorter than the sepals.
 - b. Plant not over 2 dm. high; scape short or none; leaf-blades dimorphic with the green ones deciduous..... 4. *P. HETEROPHYLLA*
 - bb. Plant 6–20 dm. high or more; scape elongate.
 - c. Inflorescence simple; leaf-blades flat.
 - d. Leaves all alike, the blades linear, 13 mm. wide; sepals 34 mm. long..... 5. *P. CARNEA*
 - dd. Leaves dimorphic, the larger with blades up to 7 cm. wide; sepals 20 mm. long..... 6. *P. KALBREYERI*
 - cc. Inflorescence laxly tripinnate; leaf-blades plicate..... 7. *P. VALERII*

1. PITCAIRNIA ATRORUBENS (Beer) Baker in Jour. Bot. 19:307. 1881.

Phlomostachys atrorubens Beer, Bromel. 48. 1857.

Puya Warszewiczii H. Wendl. ex Hook. in Bot. Mag. pl. 5225. 1861.

Pitcairnia Lamarcheana E. Morr. ex Baker, Handb. Bromel. 111. 1889.

Pitcairnia Lindenii Baker, Handb. Bromel. 112. 1889.

Pitcairnia atrorubens var. *Lamarcheana* (E. Morr. ex Baker) Mez in DC. Monogr. Phan. 9:457. 1896.

Hepetis atrorubens (Beer) Mez in DC. Monogr. Phan. 9:973. 1896.

Hepetis Lindenii (Baker) Mez in DC. Monogr. Phan. 9:974. 1896.

Plant 6–9 dm. high. Leaves about 6, some much reduced, ovate, abruptly acute, brown, other leaves 6–9 dm. long, petiolate; sheaths triangular-ovate,

brown-lepidote; petioles 2 dm. long, channeled, armed with small dark recurved spines, tomentose-lepidote beneath; blades lanceolate, acuminate, 5 dm. long, 55–60 mm. wide, entire, glabrous. Scape erect, stout, elongate. Scape-bracts with a large ovate base and long acuminate blade, subglabrous, especially the upper ones brownish purple. Inflorescence simple, subspicate, obtuse, densely many-flowered, 2–3 dm. long, 3–5 cm. thick. Rhachis finely tomentose-lepidote, wholly concealed. Floral bracts broadly ovate with a narrowly triangular divergent blade, 5–7 cm. long, much exceeding the sepals, glabrous, deep reddish purple to bright red or rarely yellowish. Flowers subsessile. Sepals oblong, abruptly acute, short-mucronate, 25 mm. long, narrowly winged near apex, minutely lanate. Petals linear, broadly acute, exceeding the stamens, unequal, to 77 mm. long, pale yellow, bearing a large bidentate scale at base. Ovary $\frac{3}{4}$ superior. Ovules long-caudate. Capsule broadly ovoid, 13–20 mm. long.

Costa Rica, Panama, Mexico (?).

CHIRIQUÍ: mountains of Chiriquí, *Warszewicz*; Boquete, Boquete District, alt. 1200 m., *Davidson* 764. COCLÉ: trail to Las Minas, north of El Valle de Antón, alt. 1000 m., *Allen* 2466.

Pitcairnia Lamarcheana has been separated as a species and then as a variety on its pale yellowish floral bracts, but it is known only from cultivation and it is not possible to say whether this difference is really significant.

2. *PITCAIRNIA OBLANCEOLATA* L. B. Smith in *Contrib. Gray Herb.* 117:26, *pl.* 2, *fig.* 18. 1937.

Climbing woody stem averaging over 1 m. long. Leaves few, erect; sheaths broadly ovate, 3–4 cm. long, dark castaneous, covered with a buff membrane of coalesced scales; petiole distinct, stout, channeled, densely serrate with dark spines to 3 mm. long; blades oblanceolate, acute, 85–95 cm. long, 105–125 mm. wide, entire, flat, glabrous or slightly flocculose beneath. Scape erect, stout, 3–4 dm. long. Scape-bracts very densely imbricate, some subfoliaceous, others vaginiform, elliptic, caudate. Inflorescence simple, densely cylindric, 3–8 dm. long, 3–4 cm. thick before anthesis. Floral bracts broadly elliptic, acute or acuminate, 7–8 cm. long, much exceeding the sepals, chartaceous, pink drying to castaneous. Flowers erect or spreading at anthesis. Pedicels stout, to 1 cm. long. Sepals oblanceolate, broadly acute and apiculate, 45 mm. long, 10 mm. wide, thin. Petals



Fig. 97
Pitcairnia atrorubens



Fig. 98
Pitcairnia oblanceolata

8 cm. long, exceeding the stamens, yellow, bearing a large truncate scale at base.
Costa Rica, Panama.

PANAMÁ: epiphytic, summit of Cerro Campana, alt. 800-1000 m., *Allen 2214*.

3. *PITCAIRNIA APHELANDRAEFLORA* Lem. in Ill. Hort. 16: Misc. 90. 1869.

Pepinia apelandraeflora (Lem.) André in Ill. Hort. 17:32, pl. 5. 1870.

Hepetis apelandriflora (Lem.) Mez in DC. Monogr. Phan. 9:973. 1896.

Stem erect, 3 dm. high, 3-5 mm. thick, becoming naked below as the leaves disintegrate. Leaves all alike, densely imbricate, spreading, 2 dm. long, disinte-



Fig. 99. *Pitcairnia apelandraeflora*

grating with age but not regularly deciduous; sheaths elliptic, about 2 cm. long, sparsely and obscurely lepidote, their margins brown and membranaceous; blades linear, caudate-acuminate, 5-7 mm. wide, narrowly channelled, glabrous, very

laxly and minutely serrulate toward apex. Scape very short. Scape-bracts imbricate, resembling the leaf-sheaths, thin. Inflorescence simple, densely spicate, few-flowered, glabrous. Floral bracts broadly ovate, thin, nerved, exceeding the sepals. Flowers erect. Pedicels very short. Sepals asymmetric, lanceolate or narrowly elliptic, 18 mm. long, ecarinate. Petals 5 cm. long, obtuse, bright red, naked or with 2 vertical folds near base. Stamens exserted. Ovary over $\frac{1}{2}$ superior. Ovules obtuse.

Amazonian Brazil, Peru, Panama.

BOCAS DEL TORO: on rock, hills behind Fish Creek, von Wedel 2282.

4. *PITCAIRNIA HETEROPHYLLA* (Lindl.) Beer, Bromel. 68. 1857.

Puya heterophylla Lindl. in Bot. Reg. 26: pl. 71. 1840.

Puya longifolia C. Morren in Ann. Soc. Agr. Bot. Gand 2:483. 1846.

Hepetis heterophylla (Lindl.) Mez in DC. Monogr. Phan. 9:973. 1896.

Flowering plant 1 dm. high or rarely to 2 dm. Leaves very numerous in a large bulb; sheaths suborbicular to ovate, deep castaneous; blades dimorphic, the outer reduced to spinose-serrate castaneous spines, the inner green, linear, filiform-acuminate, to 7 dm. long and 13 mm. wide, pale-flocculose beneath, soon glabrous, deciduous before anthesis along a straight transverse line slightly above the base, entire above that line, spinulose-serrate below it. Scape usually very short and concealed by the leaves. Scape-bracts ovate, acuminate or the lower with a dark slenderly spinose apex, thin, white-flocculose. Inflorescence simple, capitate or subspicate, 3- to 12-flowered. Floral bracts like the upper scape-bracts, entire, shorter than the sepals. Flowers erect. Pedicels 3 mm. long, obconic. Sepals narrowly subtriangular, acuminate, 3 cm. long, subulate-carinate, thin, flocculose. Petals linear, to 55 mm. long, red or sometimes white, bearing a sacciform retuse scale well above base. Ovary about half superior. Ovules long-caudate. Capsule slenderly ovoid, acute, shorter than the sepals.



Fig. 100
Pitcairnia heterophylla

Southern Mexico to Panama, Venezuela, Ecuador.

CHIRIQUÍ: forest of Cerro de Lino, above El Boquete, alt. 1300-1560 m., *Pittier* 3033; in savannas, Cerro Vaca, eastern Chiriquí, alt. 900-1136 m., *Pittier* 5373. COCLÉ: lower portion of valley and marshes along Río Antón, El Valle de Antón, alt. ca. 500 m., *Hunter & Allen* 364. CANAL ZONE: Barro Colorado Island, *Aviles* 61; forest along banks of Quebrada La Palma and Cañon of Río Chagres, alt. 70-80 m., *Dodge & Allen* 17467. INDEFINITE: *Seemann* 1564.

5. *PITCAIRNIA CARNEA* Beer in Oesterr. Bot. Zeitschr. 8:182. 1858.

Puya carnea Regel, Cat. Pl. Hort. Aksak. 117. 1860, *nomen*.

Hepetis carnea (Beer) Mez in DC. Monogr. Phan. 9:973. 1896.

Stemless, 6 dm. high. Leaves all alike, many, densely fasciculate, persistent, narrowed between sheath and blade but not actually petiolate; sheaths broadly triangular-ovate, entire, brown at base; blades linear, filiform-acuminate, 6 dm. long, 13 mm. wide, entire except for a few teeth at base, densely white-lepidote beneath, glabrous above at maturity. Scape evident, straight, soon glabrous. Scape-bracts strict, lance-triangular, acuminate, pungent, lepidote, becoming glabrous, the upper ones equaling or slightly shorter than the internodes. Inflorescence racemose, cylindric, 2 dm. long, white-floccose. Floral bracts lanceolate, acuminate, equaling or exceeding the pedicels, the lower ones 18 mm. long. Flowers erect, about 55 mm. long. Pedicels slender, erect, 10–15 mm. long. Sepals sublinear, filiform-acuminate, 34 mm. long, 4 mm. wide, often uncinat, ecarinate. Petals red, strongly recurved after anthesis, bearing a large coarsely dentate scale at base. Stamens barely exserted. Ovary $\frac{3}{4}$ superior. Ovules long-caudate.

Endemic.

Indefinite. "VERAGUAS": known only from cultivation.

6. PITCAIRNIA KALBREYERI Baker in Jour. Bot. 19:273. 1881.

Hepetis Kalbreyeri (Baker) Mez in DC. Monogr. Phan. 9:974. 1896.

Stemless, over 2 m. high. Leaves dimorphic, some much reduced with spini-form serrate blades, others elongate, their blades linear-lanceolate, acuminate, up to 7 cm. wide, entire, more or less furfuraceous beneath, narrowed at base into a distinct elongate serrate petiole. Scape erect, soon glabrous. Scape-bracts lanceolate, acuminate, spinose-serrate, shorter than the internodes. Inflorescence simple, elongate, laxly racemose, soon glabrous. Floral bracts narrowly triangular, about equaling the pedicels. Flowers spreading, slender. Pedicels slender, 15 mm. long. Sepals narrowly triangular, acuminate, 2 cm. long, ecarinate, striate. Petals linear, to 65 mm. long, red or pink, naked or with minute auricles near base. Ovary $\frac{3}{4}$ superior.

Colombia, Panama.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, alt. 1800 m., Davidson 300.

7. PITCAIRNIA VALERII Standley in Jour. Wash. Acad. 17:246. 1927.



Fig. 102
Pitcairnia
Valerii

Plant to 2 m. high. Stem 10–13 cm. long, covered by the densely imbricate leaf-bases. Leaves 10–15 dm. long, entire; sheaths triangular, 1 dm. long, densely and finely brown-appressed-lepidote; petioles 15–25 cm. long, 5 mm. wide; blades sublinear, acuminate, 30–35 mm. wide, bearing 5 or 6 narrow grooves, finely nerved, glabrous. Scape erect, short, slender, glabrous. The lower scape-bracts foliaceous, 5 dm. long, the upper 2 cm. long. Inflorescence paniculate, laxly tripinnate, 7–18 dm. long, glabrous. Pri-

mary bracts deciduous by anthesis. Axes terete, smooth, red. Branches to 33 cm. long. Racemes many-flowered. Internodes 4–10 mm. long. Floral bracts lanceolate, acuminate, shorter than the pedicels, greenish with a scarious margin. Flowers spreading or nutant. Pedicels slender, 5–7 mm. long. Sepals narrowly triangular, acuminate, 9–12 mm. long, ecarinate. Petals linear, acute, 2 cm. long, red, bearing a small suborbicular scale at base. Stamens shorter than the petals. Ovary $\frac{4}{5}$ superior. Seeds long-caudate.

Costa Rica, Panama.

PANAMÁ: summit of Cerro Campana in deep shade, alt. 1000 m., *Allen 2414*.

PITCAIRNIA SAXICOLA L. B. Smith in Contrib. Gray Herb. 117:29. 1937.

Pitcairnia fulgens A. Dietr. in Allg. Gartenzeit. 19:137. 1851, non Dietr. 1837.

Pitcairnia splendens Warscz. ex A. Dietr. in Allg. Gartenzeit. 19:176. 1851, non Poit. 1836.

This species is distinguished by narrow deciduous leaf-blades, large imbricate floral bracts and long scape and inflorescence. The original description drawn from cultivated material gave Guatemala as its home without indicating any more definite locality. However, herbarium specimens are labelled as from Chiriquí in Panama. Warszewicz, the collector, had been in both Guatemala and Panama by 1851, so it is not possible to eliminate Panama on the basis of the date. A second collection of the species from southern Mexico, however, makes Guatemala seem much more probable as the origin of the type.

ARTIFICIAL KEY TO THE PANAMANIAN SPECIES OF *TILLANDSIA*, *VRIESIA*,
THECOPHYLLUM AND *GUZMANIA*

- a. Spikes with flowers distichous or secund, or else the inflorescence reduced to a single flower.
 - b. Sepals asymmetric, free, broadest at middle or near the apex, not over 10 mm. long. TILLANDSIA spp. 9–12
 - bb. Sepals symmetric or, if slightly asymmetric, ovate or lanceolate and broadest near the base.
 - c. Inflorescence simple and bearing but a single series of bracts, or reduced to a single flower, either terminal, axillary or pseudo-axillary.
 - d. Plant long-caulescent, slender, leaves filiform. TILLANDSIA sp. 8
 - dd. Plant stemless.
 - e. Flowers secund. VRIESIA spp. 4–8
 - ee. Flowers not secund.
 - f. Floral bracts less than twice as long as the internodes, spreading. TILLANDSIA sp. 13
 - ff. Floral bracts at least twice as long as the internodes.
 - g. Leaf-blades ligulate.
 - h. Floral bracts carinate toward apex.
 - i. Scape-bracts distichous, carinate; floral bracts curved out at mid-keel. TILLANDSIA sp. 14
 - ii. Scape-bracts polystichous, ecarinate; floral bracts curved in at mid-keel. VRIESIA sp. 2
 - hh. Floral bracts broadly convex and ecarinate.
 - i. Floral bracts appearing rugose, at least under a lens, thick. VRIESIA spp. 3–4
 - ii. Floral bracts even or nerved but not rugose; inflorescences several and lateral in each rosette. TILLANDSIA sp. 5
 - gg. Leaf-blades narrowly triangular or linear, acuminate.
 - h. Leaf-sheaths inflated and forming a pseudobulb.

- i. Floral bracts glabrous or obscurely lepidote, even or nearly so..... TILLANDSIA sp. 18
- ii. Floral bracts densely lepidote, nerved..... TILLANDSIA spp. 22-24
- hh. Leaf-sheaths nearly or quite flat, not forming a pseudobulb.
 - i. Floral bracts coriaceous or subcoriaceous, at least the larger and central part of each one.
 - j. Flowers spreading, separated..... TILLANDSIA sp. 7
 - jj. Flowers erect or suberect, contiguous.
 - k. Leaf-sheaths red-striate; spike strongly complanate..... TILLANDSIA sp. 6
 - kk. Leaf-sheaths not striate, dark castaneous at least toward base.
 - l. Spike terete..... TILLANDSIA sp. 17
 - ll. Spike more or less complanate..... TILLANDSIA spp. 19-21
 - ii. Floral bracts subchartaceous to membranaceous..... TILLANDSIA spp. 25-27
 - cc. Inflorescence of 2 or more branches.
 - d. Flowers secund.
 - e. Pedicels slender, 1-2 cm. long; sepals 7-11 mm. long..... THECOPHYLLUM sp. 5
 - ee. Pedicels stout; sepals 25-45 mm. long.
 - f. Floral bracts abruptly acute; rhachis even..... VRIESIA sp. 6
 - ff. Floral bracts acuminate; rhachis verrucose just below the nodes..... VRIESIA sp. 8
 - dd. Flowers not secund.
 - e. Floral bracts less than twice as long as the internodes, spreading..... TILLANDSIA sp. 13
 - ee. Floral bracts at least twice as long as the internodes.
 - f. Leaf-sheaths inflated and forming a pseudobulb.
 - g. Floral bracts glabrous or obscurely lepidote, even or nearly so..... TILLANDSIA sp. 18
 - gg. Floral bracts densely lepidote, nerved..... TILLANDSIA spp. 23-24
 - ff. Leaf-sheaths nearly or quite flat, not forming a pseudobulb.
 - h. Leaf-blades linear-subulate to filiform; leaves closely fasciculate..... TILLANDSIA spp. 15-16
 - hh. Leaf-blades definitely if narrowly triangular or ligulate.
 - i. Leaf-blades ligulate.
 - j. Sepals broadly elliptic, obtuse, 21 mm. wide..... VRIESIA sp. 1
 - jj. Sepals much narrower..... TILLANDSIA spp. 1-3
 - ii. Leaf-blades narrowly triangular.
 - j. Floral bracts coriaceous or subcoriaceous, at least the larger and central part of each one.
 - k. Spikes terete..... TILLANDSIA sp. 17
 - kk. Spikes more or less complanate..... TILLANDSIA spp. 19-21
 - jj. Floral bracts subchartaceous to membranaceous.
 - k. Leaf-sheaths castaneous, darker than the blades; floral bracts 25-35 mm. long..... TILLANDSIA sp. 25
 - kk. Leaf-sheaths concolorous with the blades.
 - l. Spikes 1-2 cm. wide; plant 2-6 dm. high..... TILLANDSIA sp. 26
 - ll. Spikes 12 mm. wide; plant 1 m. high..... TILLANDSIA sp. 4
 - aa. Spikes with flowers polystichous.
 - b. Inflorescence simple and bearing but a single series of bracts.
 - c. Leaf-blades filiform-subulate; leaves closely fasciculate; floral bracts coriaceous..... TILLANDSIA sp. 16
 - cc. Leaf-blades narrowly triangular to ligulate, definitely flattened..... GUZMANIA spp. 1-7
 - bb. Inflorescence compound (when perfect flowers are single in the axil of each primary bract, the presence of floral bracts indicates a compound inflorescence).
 - c. Branches of the inflorescence nearly or quite aborted with the flowers fascicled or solitary in the axils of the primary bracts..... THECOPHYLLUM spp. 1-4
 - cc. Branches of the inflorescence well developed.
 - d. Floral bracts equaling or exceeding the sepals..... GUZMANIA spp. 8-9
 - dd. Floral bracts exceeded by the sepals.

- e. Pedicels 1-2 cm. long, slender..... *THECOPHYLLUM* sp. 5
 ee. Pedicels short and stout or almost lacking.
 f. Sepals nearly as broad as long, free..... *THECOPHYLLUM* sp. 6
 ff. Sepals at least twice as long as broad..... *GUZMANIA* spp. 10-13

2. *TILLANDSIA* L.

TILLANDSIA L. Sp. Pl. 286. 1753.

Renealmia L. Sp. Pl. 286. 1753.

Bonaparteia R. & P. Fl. Peruv. 3:38. 1802.

Acanthospora Spreng. Anl. ed. 2, 2:255. 1817.

Misandra Dietr. Lex. Nachtr. 5:102. 1819, non Commerson, 1789.

Dendropogon Raf. Neog. 3. 1825.

Bonaparteia Sweet, Hort. Brit. ed. 3. 706. 1839.

Strepsia Nutt. ex Steud. Nomencl. Bot. ed. 2, 2:645. 1841.

Allardtia A. Dietr. in Allg. Gartenzeit. 20:241. 1852.

Anoplophytum Beer in Flora 37:346. 1854.

Diaphoranthema Beer in Flora 37:349. 1854.

Phytarrhiza de Vis. in Mem. Ist. Veneto 5:340. 1855.

Platystachys Beer, Bromel. 18, 80. 1857.

Pityrophyllum Beer, Bromel. 17, 79. 1857.

Wallisia E. Morr. in Belg. Hort. 20:97. 1870.

Cipuroopsis Ule in Verhandl. Bot. Ver. Brandenburg 48:148. 1907.

Caulесcent or acaulescent herbs of very variable habit. Leaves rosulate or fasciculate or distributed along a stem, polystichous or distichous, entire, blades ligulate or subtriangular or filiform. Scape usually distinct. Inflorescence various, usually of distichous-flowered spikes or sometimes reduced to a single polystichous-flowered spike by the reduction of the spikes to single flowers or rarely the whole inflorescence reduced to a single flower. Flowers perfect. Sepals usually symmetric, free, or equally or posteriorly joined. Petals free, naked or rarely with vertical folds. Stamens of various lengths relative to the petals and pistil. Ovary superior, glabrous. Ovules usually many and caudate. Capsule septicidal. Seeds erect, narrowly cylindric or fusiform, the plumose appendage white, straight, basal.

- a. Stamens equaling or shorter than the petals.
 b. Sepals symmetric, or if slightly asymmetric, ovate or lanceolate, broadest near base.
 c. Stamens exerted from the throat of the corolla; style slender, much longer than the ovary..... Subgenus *ALLARDTIA*
 d. Inflorescence compound, central.
 e. Leaf-blades ligulate; spikes lanceolate or elliptic.
 f. Spikes dense or subdense; floral bracts about equaling the sepals.
 g. Sepals 25 mm. or longer; primary bracts all much shorter than the branches..... 1. *T. RUBRA*
 gg. Sepals 15-20 mm. long; lower primary bracts exceeding the branches..... 2. *T. EXCELSA*
 ff. Spikes lax; floral bracts much shorter than the sepals..... 3. *T. SINGULARIS*
 ee. Leaf-blades narrowly triangular; spikes linear, 15 cm. long, 12 mm. wide..... 4. *T. SUBIMBRICATA*
 dd. Inflorescences simple, numerous and axillary in each rosette..... 5. *T. COMPLANATA*
 cc. Stamens deeply included; style short and stout; inflorescence simple in the Panamanian species.
 f. Petal-blades broad, ovate or elliptic, showy..... Subgenus *PHYTARRHIZA*
 g. Flowers and their bracts suberect, densely imbricate..... 6. *T. ANCEPS*

- gg. Flowers and their bracts spreading; inflorescence lax..... 7. *T. MONADELPHA*
 - ff. Petal-blades narrow, elliptic, inconspicuous; plants moss-like Subgenus *DIAPHORANTHEMA*
 - 8. *T. USNEOIDES*
- bb. Sepals asymmetric, free, oblong or broadest near apex, not over 10 mm. long Subgenus *PSEUDO-CATOPSIS*
- c. Floral bracts suborbicular, much exceeding the sepals, membranaceous; inflorescence simple or few-branched..... 9. *T. CRISPA*
- cc. Floral bracts barely if at all exceeding the sepals, firmer; inflorescence amply compound.
- d. Floral bracts equaling or exceeding the sepals, glabrous or subglabrous; leaf-blades ligulate..... 10. *T. SPICULOSA*
- dd. Floral bracts shorter than the sepals; leaf-blades narrowly triangular.
- e. Primary bracts at least half as long as the axillary spikes; flowers spreading; floral bracts densely lepidote..... 11. *T. ADPRESSA*
- ee. Primary bracts much shorter than the axillary spikes; flowers nearly erect; floral bracts subglabrous..... 12. *T. GUANACASTENSIS*
- aa. Stamens longer than the petals..... Subgenus *PLATYSTACHYS*
- b. Floral bracts much less than twice as long as the internodes; flowers spreading..... 13. *T. FLEXUOSA*
- bb. Floral bracts at least twice as long as the internodes; spikes usually dense.
- c. Leaf-blades ligulate; scapes several and axillary in each rosette..... 14. *T. MULTICAULIS*
- cc. Leaf-blades narrowly triangular or linear.
- d. Floral bracts coriaceous or subcoriaceous.
- e. Leaf-blades linear-subulate; leaves closely fasciculate; leaf-sheaths triangular with abruptly auricled bases.
- f. Spikes arching-recurved, linear; floral bracts barely imbricate..... 15. *T. FESTUCOIDES*
- ff. Spikes erect (or inflorescence simple), elliptic or lanceolate, dense..... 16. *T. JUNCEA*
- ee. Leaf-blades definitely if narrowly triangular; leaf-sheaths usually ovate or elliptic without auricled bases.
- f. Spikes terete 17. *T. ACOSTAE*
- ff. Spikes more or less complanate.
- g. Spikes linear-lanceolate, not over 12 mm. wide; leaf-sheaths scarcely darker than the blades, inflated..... 18. *T. BALBISIANA*
- gg. Spikes lance-elliptic, ovate or oblong, 12-40 mm. wide; leaf-sheaths castaneous, much darker than the blades.
- h. Sepals alate; bracts subinvolucrate below the inflorescence..... 19. *T. PUNCTULATA*
- hh. Sepals merely carinate; bracts not at all involucrate.
- i. Sides of the spikes more or less convex; floral bracts ample..... 20. *T. FASCICULATA*
- ii. Sides of the spikes flat; floral bracts narrow; primary bracts scarcely larger than the floral..... 21. *T. MELANOCRATER*
- dd. Floral bracts subchartaceous to membranaceous.
- e. Leaf-sheaths inflated and forming a pseudobulb, the inner ones closely enfolding the scape.
- f. Sepals exceeding the floral bracts..... 22. *T. SUBULIFERA*
- ff. Sepals equaling or shorter than the floral bracts.
- g. Leaf-sheaths variegated..... 23. *T. BUTZII*
- gg. Leaf-sheaths green, concolorous or with only a narrow margin of red or purple..... 24. *T. BULBOSA*
- ee. Leaf-sheaths nearly flat and forming a crateriform rosette.
- f. Floral bracts narrow, exposing the rhachis at anthesis.
- g. Leaf-sheaths dark castaneous; floral bracts 25-35 mm. long..... 25. *T. INCURVA*
- gg. Leaf-sheaths green like the blades; floral bracts 20 mm. long..... 26. *T. VALENZUELANA*
- ff. Floral bracts broad, densely imbricate, incurved, rugulose and blackish when dry..... 27. *T. KEGELIANA*

1. *TILLANDSIA RUBRA* R. & P. Fl. Peruv. 3:40. 1802.

Tillandsia paniculata Schlecht. & Cham. in Linnaea 6:54. 1831, non L. 1762.

Plant 1–2 m. high. Leaves many in a dense crateriform rosette, 6–10 dm. long; sheaths subelliptic, densely brown-punctulate-lepidote; blades ligulate, acuminate, to 8 cm. wide, typically subglabrous. Scape erect, stout. Scape-bracts densely imbricate, foliaceous. Inflorescence lax, ample, pinnately compound with simple or divided branches. Primary bracts like the upper scape-bracts, much shorter than the branches but much larger than the floral bracts. Spikes lanceolate, acute, complanate, dense, 1–3 dm. long, 5 cm. wide, often spreading or recurved, stipitate with sterile bracts at base. Floral bracts narrowly obovate, keeled toward the apex, glabrous, even, coriaceous at maturity, about equaling the sepals. Flowers erect, short-pedicellate. Sepals lance-oblong, 25–45 mm. long, carinate, equally subfree. Petals slightly exceeding the stamens.



Fig. 103
Tillandsia rubra

Mexico and the West Indies to Venezuela, Peru and Bolivia; apparently represented in Panama only by the following:

TILLANDSIA RUBRA var. *COSTARICENSIS* (Mez) Mez in Pflanzenreich, 4: Fam. 32:458. 1935.

Tillandsia paniculata Schlecht. & Cham. var. *costaricensis* Mez in DC. Monogr. Phan. 9:703. 1896.

Plant much smaller in all its parts. Leaves rather densely cinereous-lepidote beneath.

Costa Rica and Panama.

CHIRIQUÍ: Boquete, Boquete District, alt. 1150 m., Davidson 825.

2. *TILLANDSIA EXCELSA* Griseb. Fl. Brit. W. Ind. 597. 1864.

Tillandsia costaricana Mez & Wercklé in Bull. Herb. Boiss. II. 3:143. 1903.

Often over 1 m. high. Leaves densely rosulate, 45 cm. long, obscurely punctulate-lepidote, light green, sometimes suffused or marked with red or purple; sheaths conspicuous, suborbicular; blades ligulate, acute, to 6 cm. wide. Scape erect, glabrous. Scape-bracts foliaceous, densely imbricate. Inflorescence barely or amply tripinnate, pyramidal, red, glabrous. Primary bracts large and foliaceous, the lower ones exceeding the branches. Secondary bracts narrowly lanceolate, slightly shorter than the spikes. Spikes lanceolate or elliptic, acute, dense, 8-flowered or usually less. Floral bracts suberect, 2 to 3 times as long as the internodes but so narrow as to expose the rhachis, acute, exceeding the sepals, convex, ecarinate, coriaceous, even or nerved. Flowers subsessile, 25–30 mm. long. Sepals linear-lanceolate, acute, 15–20 mm. long, subfree. Petals violet. Stamens included. Capsule cylindric, 3 cm. long.

Central America, Cuba, Jamaica.

BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, alt. ca. 10–

50 m., Woodson, Allen & Seibert 1890. CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, alt. 1800 m., Davidson 282.

3. *TILLANDSIA SINGULARIS* Mez & Wercklé in Bull. Herb. Boiss. II. 5:103. 1905.

Plant 3–4 dm. high. Leaves rosulate, 15–25 cm. long, obscurely punctulate-lepidote; sheaths elliptic, dark castaneous with a broad pale margin; blades ligulate,



Fig. 104
Tillandsia singularis

broadly rounded and apiculate, 2–3 cm. wide, green. Scape slender, erect, about equaling the leaves or shorter. Scape-bracts imbricate, lance-elliptic, apiculate, bright red. Inflorescence slenderly pyramidal, laxly bipinnate, 15–19 cm. long, glabrous, bright red. Primary bracts like the scape-bracts, about half as long as the branches. Spikes suberect to spreading, short-stipitate with no sterile bracts at base, 4–6 cm. long, laxly 6- to 11-flowered. Rhachis slender, slightly geniculate. Floral bracts elliptic, much shorter

than the sepals, ecarinate, membranaceous, nerved. Flowers spreading, short-pedicellate. Sepals oblong, obtuse, subfree, 9–10 mm. long. Petals ligulate, 11–12 mm. long. Stamens included.

Costa Rica, Panama.

COCLÉ: region north of El Valle de Antón, alt. ca. 1000 m., Allen 2898.

4. *TILLANDSIA SUBIMBRICATA* Baker in Jour. Bot. 25:304. 1887.

Tillandsia orthorhachis Mez & C. F. Baker in Bull. Torrey Bot. Club 30:435. 1903.



Fig. 105
Tillandsia subimbricata

Plant 1 m. high. Leaves many in a utriculate rosette, to 8 dm. long, densely punctulate-lepidote; sheaths ovate, large, not inflated, blades recurving, narrowly triangular, subulate-acuminate, 4 cm. wide. Scape erect, 1 cm. thick. Scape-bracts imbricate, the lower ones foliaceous with long reflexed laminae, the upper ovate and usually apiculate or with short filiform erect laminae. Inflorescence laxly compound. Branches simple or rarely the lowest divided, curved-ascending. Primary bracts like the upper scape-bracts, much shorter than the branches. Spikes linear, complanate, to 20-flowered with several sterile bracts at base, 15 cm. long, 12 mm. wide. Rhachis nearly straight, slender, glabrous. Floral bracts erect, 2 to 3 times as long as the internodes or sometimes less, exposing the rhachis, narrowly ovate, obtuse or apiculate, 18–20 mm. long, exceeding the sepals, subchartaceous, glabrous, strongly nerved. Flowers subsessile. Sepals narrowly elliptic, obtuse, equally subfree. Petals 25 mm. long, blue or lilac. Stamens included. Capsule slenderly cylindric, 3–4 cm. long.

Yucatan, Nicaragua, Panama, Cuba, Jamaica, Trinidad, Colombia.

PANAMÁ: near Punta Paitilla, Standley 26254; along the Corozal Road near Panamá, Standley 26837; Río Tapia, Standley 28255. INDEFINITE: H. A. Dunn in hb. Foster 1169.

5. *TILLANDSIA COMPLANATA* Benth. Bot. Voy. Sulph. 173. 1846.

Tillandsia axillaris Griseb. Fl. Brit. W. Ind. 597. 1864.

Leaves many in a dense rosette, 3-4 dm. or rarely longer, mostly exceeding the inflorescences, spotted, streaked or suffused with dark purple especially toward base; sheaths elliptic or narrowly ovate, 10-16 cm. long, densely brown-appressed-lepidote; blades ligulate, abruptly acute or subobtusely, apiculate, 3-5 cm. wide,



Fig. 106. *Tillandsia complanata*

obscurely punctulate-lepidote, soon glabrous above. Scapes many from the axils of the leaves, ascending, 1-2 mm. thick above the flattened base, glabrous. Scape-bracts many, erect, usually imbricate, narrowly lanceolate, subchartaceous, nearly or quite glabrous. Inflorescences simple, lanceolate or linear, acute, 4- to 24-flowered, to 8 cm. long, 15-20 mm. wide, usually complanate, glabrous. Floral bracts imbricate, elliptic, obtuse, 15-25 mm. long, exceeding the sepals,

ecarinate, coriaceous or subcoriaceous, even or nerved, often rose to purple. Flowers subsessile. Sepals lanceolate, acute, the posterior ones carinate and usually much connate. Petals about 2 cm. long, rose, purple or blue, the blade suberect. Stamens slightly shorter than the petals. Capsule slenderly cylindric, 4 cm. long.

Costa Rica, Panama, West Indies, British Guiana to Peru and Bolivia.

CHIRIQUÍ: vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., Woodson & Schery 602; south slope of Volcán de Chiriquí, Boquete District, alt. 3000 m., Terry 1369.

6. *TILLANDSIA ANCEPS* Lodd. Bot. Cab. pl. 771. 1823.

Platystachys anceps (Lodd.) Beer, Bromel. 80. 1857.

Vriesea anceps (Lodd.) Lemaire in Ill. Hort. 6: Misc. 15. 1859.

Tillandsia xiphostachys Griseb. in Nachr. Ges. Wiss. Gött. 1864:14. 1865, in part.

Phytarrhiza anceps (Lodd.) E. Morr. in Belg. Hort. 29:368. 1879.

Vriesea Schlechtendablii Wittm. in Engler's Bot. Jahrb. 11:69. 1889, excl. syn.

Vriesea Schlechtendablii var. *alba* Wittm. l. c.

Tillandsia lineatifolia Mez in DC. Monogr. Phan. 9:686. 1896.

Leaves many, densely rosulate, 15-40 cm. long, equaling or exceeding the inflorescence, densely and minutely pale-appressed-lepidote, green; sheaths triangular-ovate, red-striate; blades recurving, narrowly triangular, acuminate, 7-12 mm. wide. Scape erect, very short, stout. Scape-bracts densely imbricate, ovate, acute or the lowest with a stiff erect linear blade, much smaller than the floral bracts, coriaceous, even, glabrous. Inflorescence simple, elliptic, strongly com-

Fig. 107. *Tillandsia anceps*

planate, 10–15 cm. long, 55 mm. wide, 10- to 20-flowered, glabrous. Floral bracts densely imbricate, triangular-acute, to 4 cm. long, much exceeding the sepals, carinate, coriaceous, even, green or pale rose with greenish margins. Flowers short-pedicellate. Sepals narrowly lanceolate, acute, 3 cm. long, equally subfree, carinate. Petals more than twice as long as the sepals, the claw linear, white, the blade spreading, lance-elliptic, acute, blue or rarely white. Stamens deeply included, exceeding the style. Capsule slenderly cylindric, shorter than the sepals.

Honduras, Costa Rica, Panama, Trinidad, British Guiana, Venezuela, Colombia.

CANAL ZONE: between Frijoles and Monte Lirio, alt. 30 m., Killip 12144; Barro Colorado Island, Kenoyer 215; Aviles 7, 13; Bailey 370; Shattuck 560; near Río Medio, Miller 1754.

This species has been confused with *Tillandsia compressa* Bert., a synonym of *T. fasciculata*.

7. *TILLANDSIA MONADELPHA* (E. Morr.) Baker in Jour. Bot. 25:281. 1887.

Phytarribiza monadelphæ E. Morr. in Belg. Hort. 32:168. 1882.

Tillandsia graminifolia Baker in Jour. Bot. 25:281. 1887.

Tillandsia monobotrya Mez in Fedde Rep. Spec. Nov. 16:77. 1919.

Tillandsia digitata sensu Standl. in Smithson. Misc. Coll. 78⁸:12. 1927, non Mez, 1896.

Fig. 108. *Tillandsia monadelphæ*

Plant 35 cm. high. Leaves densely rosulate, 2 dm. long, obscurely punctulate-lepidote; sheaths ovate; blades very narrowly triangular, 10–15 mm. wide. Scape erect, slender, glabrous. Scape-bracts lance-elliptic, imbricate, lepidote at apex. Inflorescence simple, distichous, oblong, much compressed, about 22-flowered, lax by the spreading of the flowers, 13 cm. long. Rhachis straight, angled, thickened at the nodes. Floral bracts ovate, acute, 17 mm. long, equaling the sepals, coriaceous or subcoriaceous, carinate, striate, soon glabrous. Flowers sessile, 30 mm. long. Sepals equally short-connate, lance-elliptic, carinate, glabrous. Petals white, the blade ovate, reflexed. Stamens deeply included, exceeding the style. Capsule slenderly cylindric, 4–7 cm. long.

Central America, Colombia and Ecuador to Guiana and Trinidad.

COCLÉ: north of El Valle de Antón, near La Mesa, alt. ca. 1000 m., *Allen* 2782. CANAL ZONE: hills around the Agua Clara Reservoir, near Gatún, alt. 20–30 m., *Pittier* 2658; wet forest, Barro Colorado Island, Gatún Lake, alt. ca. 120 m., *Standley* 41169; Barro Colorado Island, *Kenoyer* 214; westerly arm of Quebrada Salamanca, alt. 75 m., *Dodge*, *Steyermark* & *Allen* 17024. DARIÉN: Cana-Cuasi Trail (Camp 2), Chepigana District, alt. 600 m., *Terry* 1546.

8. *TILLANDSIA USNEOIDES* L. Sp. Pl. ed. 2. 411. 1762.

Renalmia usneoides L. Sp. Pl. 287. 1753.

Tillandsia trichoides HBK. Nov. Gen. & Sp. 1:290. 1816.

Dendropogon usneoides (L.) Raf. Fl. Tellur. 4:25. 1838.

Strepsia usneoides (L.) Steud. Nomencl. Bot. ed. 2, 2:645. 1841.

Tillandsia crinita Willd. ex Beer, Bromel. 152. 1857.



Fig. 109. *Tillandsia usneoides*

Growing pendent from trees in slender branching strands up to 8 m. long. Roots absent. Stem less than 1 mm. thick, sympodial, the internodes 3–6 cm. long with only the extreme base covered by the leaves, curved. Leaves distichous, 5 cm. long, densely lepidote; sheaths elliptic, 8 mm. long; blades filiform, less than 1 mm. thick. Scape lacking. Inflorescence reduced to a single flower. Floral bract shorter than the sepals, ovate, lepidote. Sepals narrowly ovate, acute, to 7 mm. long, thin, nerved, glabrous, equally short-connate.

Petals narrow, 9–11 mm. long, pale green or blue. Stamens deeply included, exceeding the pistil. Capsule cylindric, to 25 mm. long.

Virginia to Texas along the coast and south to central Argentina and Chile. "Spanish Moss" of the southeastern United States.

BOCAS DEL TORO: hillside forest, near Olivia, *Woodson* & *Schery* 1032; Water Valley, near Chiriquí Lagoon, *von Wedel* 1454.

9. *TILLANDSIA CRISPA* (Baker) Mez in DC. Monogr. Phan. 9:739. 1896.

Guzmania crispa Baker in Jour. Bot. 25:173. 1887.

Tillandsia undulifolia Mez in DC. Monogr. Phan. 9:740. 1896.

Tillandsia plicatifolia Ule in Verhandl. Bot. Ver. Brandenburg 48:144. 1907.



Fig. 110
Tillandsia
crispata

Plant 1–3 dm. high. Leaves many, densely rosulate, finely appressed-lepidote; sheaths large, broadly elliptic, brown-lepidote; blades very narrowly triangular, undulate-crisped. Scape erect or slightly curved, slender. Scape-bracts imbricate, elliptic, somewhat inflated, apiculate or caudate, appressed-lepidote. Inflorescence simple or digitate from several spikes. Spikes oblong, 6- to 36-flowered, 3–8 cm. long, 15–25 mm. wide. Floral bracts imbricate, suborbicular, 9–15 mm. long, exceeding the sepals, inflated-convex, membranaceous, lepidote. Flowers sessile. Sepals broadly elliptic, asymmetric, coriaceous, even, sparingly lepidote or glabrous. Petals exceeding the sepals, coherent. Stamens and pistil included.

Panama, Colombia, Ecuador, Peru.

DARIÉN: Cerro de Garagará, Sambú Basin, southern Darién, alt. 500–974 m., *Pittier* 5653.

10. *TILLANDSIA SPICULOSA* Griseb. in Nachr. Ges. Wiss. Gött. 1864:17. 1865.

Tillandsia micrantha Baker ex Rusby in Bull. Torrey Bot. Club 29:698. 1902, non Baker, 1887.

Plant to 8 dm. high. Leaves rosulate, 3–4 dm. long, obscurely punctulate-lepidote, often irregularly purple-spotted; sheaths large, ovate, dark brown; blades ligulate, rounded and apiculate or acute, 2–4 cm. wide. Scape erect, glabrous, often much exceeding the leaves. Scape-bracts elliptic, apiculate or short-caudate, about equaling the internodes or the upper ones slightly shorter, punctulate-lepidote. Inflorescence tripinnate or if bipinnate the branches not over 7 cm. long, lax. Primary bracts narrowly ovate, apiculate, much shorter than the branches. Spikes spreading, linear, often curved, dense, to 24-flowered, 9 cm. long, 6–9 mm. wide, usually long-stipitate with sterile bracts at the base. Floral bracts broadly ovate, 6–9 or rarely 5 mm. long, equaling or slightly exceeding the sepals, convex, ecarinate, coriaceous, nearly or quite even, scantily lepidote or glabrous. Sepals asymmetric, broadly elliptic, glabrous. Petals orange or yellow. Stamens included. Capsule slenderly cylindric, 22 mm. long.

Represented in Panama only by the following:

TILLANDSIA SPICULOSA var. *PALMANA* (Mez) L. B. Smith in Contrib. Gray Herb. 89:14. 1930.

Tillandsia palmana Mez in Engler's Bot. Jahrb. 30: Beibl. 67:9. 1901.

Sterile bases of the branches shorter than the primary bracts. Leaves rounded and apiculate.

Costa Rica, Panama.

PANAMÁ: cloud forest, hills above Campana, alt. 600–800 m., *Allen* 1878; Cerro Campana, alt. 1000 m., *Allen* 2435.

11. *TILLANDSIA ADDRESSA* André, Enum. Bromel. 6. 13 Dec. 1888; in Rev. Hortic. 60:566. 16 Dec. 1888.

Catopsis Schumanniana Wittm. in Engler's Bot. Jahrb. 11:70. 1889.

Tillandsia Schumanniana (Wittm.) Mez in DC. Monogr. Phan. 9:740. 1896.

Very variable, 2–5 dm. high. Leaves many, rosulate, usually forming an ovoid pseudobulb, 15–30 cm. long, densely punctulate-lepidote, sheaths broad, dark brown; blades narrowly triangular, involute-subulate toward apex, not over 20 mm. wide, pale-lepidote. Scape erect or nearly so, lepidote. Scape-bracts ovate-oblong, long-caudate, their bases usually equaling or exceeding the internodes. Inflorescence narrow, bipinnate, of 4–12 spikes, erect to pendulous. Axis straight to geniculate, lepidote. Primary bracts narrow, attenuate to caudate, densely lepidote, usually equaling or exceeding the spikes, always at least half as long. Spikes with 8–12 distichous flowers. Floral bracts shorter than the sepals, ovate, acute, densely lepidote. Flowers sessile, spreading. Sepals scarcely over 5 mm. long, strongly asymmetric, obovate, densely lepidote. Capsule cylindric, apiculate, 20–25 mm. long.

Represented in Panama only by the following:

TILLANDSIA ADDRESSA var. *TONDUZIANA* (Mez) L. B. Smith in Contrib. Gray Herb. 89:8. 1930.

Tillandsia Tonduziana Mez in Engler's Bot. Jahrb. 30: Beibl. 67:9. 1901.

Inflorescence open, elongate, the spikes spreading or reflexed at maturity.

Costa Rica, Panama.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, alt. 1800 m., Davidson 280.

12. *TILLANDSIA GUANACASTENSIS* Standl. in Jour. Wash. Acad. 17:247. 1927.



Fig. 111
Tillandsia
guanacastensis

Plant 15–20 cm. high. Leaves about 25, densely rosulate, 10–20 cm. long, densely gray-appressed-lepidote; sheaths 2–3 cm. wide, broadly ovate; blades narrowly triangular, 10 mm. wide, involute. Scape erect, largely concealed by the leaves. Scape-bracts about equaling the internodes, ovate-elliptic, apiculate, pale-lepidote. Inflorescence digitate or pinnate, from 2 to 9 spikes, equaling or slightly exceeding the leaves. Primary bracts like the scape-bracts, extending no higher than the lowest flower of the spike. Spikes densely 12- to 22-flowered, straight, nearly erect, 3–6 cm. long, about 1 cm. wide. Floral bracts 4 mm. long, distinctly shorter than the sepals, convex, ecarinate, ovate, obtuse, sparsely pale-lepidote, even, thin. Flowers sessile, nearly erect. Sepals obovate, asymmetric, 5–6 mm. long, emarginate, sparsely lepidote. Petals 6 mm. long, yellowish white. Stamens included. Capsule slenderly cylindric, 18–20 mm. long.

Costa Rica, Panama.

COCLÉ: vicinity of El Valle de Antón, alt. ca. 600 m., Allen 2060.

13. *TILLANDSIA FLEXUOSA* Sw. Prodr. 56. 1788.*Tillandsia tenuifolia* sensu Jacq. Sel. Stirp. Am. 92. 1763, non L. 1762.*Tillandsia flexuosa* β . *fasciata* Lindl. in Bot. Reg. 9: under pl. 749. 1823.*Tillandsia aloifolia* Hook. Exot. Fl. pl. 205. 1826.*Tillandsia patens* Willd. ex Schult. in R. & S. Syst. Veg. 7:1229. 1830.*Vriesea aloifolia* (Hook.) Beer, Bromel. 95. 1857.*Vriesea tenuifolia* Beer, Bromel. 96. 1857, in part.*Platystachys patens* (Willd.) K. Koch in Ind. Sem. Hort. Berol. 1873: App. 4:5. 1874.*Tillandsia flexuosa* var. *vivipara* André, Bromel. Andr. 82. 1889.

Plant 2–15 dm. high. Leaves 10–20 in a dense often subbulbous rosette, 2–5 dm. long, densely pale-appressed-lepidote, usually marked with broad white transverse bands, the outer bladeless, squamiform; sheaths ovate, very large but merging with the blade; blades narrowly triangular, about 25 mm. wide, acuminate, then abruptly acute, curved, stiff. Scape erect, slender, glabrous. Scape-bracts erect, tubular-involute, elliptic, lepidote, at least the upper ones shorter than the inter-

Fig. 112. *Tillandsia flexuosa*

nodes. Inflorescence simple or very laxly bipinnate. Primary bracts like the upper scape-bracts, much shorter than the sterile bases of the axillary branches. Branches ascending, to 4 dm. long, very lax. Rhachis slender, flexuous, angled, glabrous. Floral bracts elliptic, acute, 2–3 cm. long, equaling or shorter than the sepals, ecarinate, chartaceous, nerved, lepidote. Flowers spreading. Pedicels to 7 mm.

long. Sepals narrowly elliptic, obtuse, 2–3 cm. long, free, sparsely lepidote or glabrous. Petals tubular-erect, to 4 cm. long, white, rose or purple. Stamens exerted. Capsule slenderly cylindric, to 7 cm. long.

Southern Florida, West Indies, Panama, Colombia, Venezuela, Guiana.

PANAMÁ: Bella Vista, sea level, Killip 12042; near Punta Paitilla, Standley 26248, 26262, 26263, 30794; along the Corozal Road, near Panamá, Standley 26838; vicinity of Juan Franco Race Track, near Panamá, Standley 27787; Taboga Island, Standley 27967; Río Tapia, Standley 28292; between Las Sabanas and Matias Hernández, Standley 31904; Las Sabanas, Zetek 901; Isla Taboga, alt. ca. 0–186 m., Woodson, Allen & Seibert 1488; Lefevre Park, near Panamá City, Bartlett & Lasser 16324; wet savanna east of Panamá City, near La Jagua, Bartlett & Lasser 16391. CANAL ZONE: Balboa, Standley 25499. INDEFINITE: Hayes.

14. *TILLANDSIA MULTICAULIS* Steud. Nomencl. Bot. ed. 2, 2:688. 1841.

Tillandsia caespitosa Schlecht. & Cham. in Linnaea 6:54. 1831, non Le Conte, 1828.

Tillandsia Schlechtendalii Baker in Jour. Bot. 26:49. 1888.

Vriesea Schlechtendalii (Baker) Wittm. in Engler's Bot. Jahrb. 14: Beibl. 32:8. 1891.

Leaves many in a dense rosette, 3–4 dm. long, exceeding the inflorescences, densely but obscurely brown-punctulate-lepidote; sheaths elliptic, 12 cm. long, purple or castaneous on the inside; blades ligulate, acute and apiculate, 25–35 mm. wide. Scapes several from the axils of the leaves, erect, 5 mm. thick, glabrous. Scape-bracts distichous, imbricate, broadly elliptic, acute, incurved, carinate, 2–4 cm. long with the smallest below, glabrous, even, subcoriaceous, bright red. Inflorescences simple, lanceolate, acute, strongly complanate, 9- to 12-flowered,



Fig. 113. *Tillandsia multicaulis*

14 cm. long, 4–6 cm. wide, glabrous. Floral bracts like the scape-bracts, densely imbricate, 5 cm. long, 4 cm. wide, much exceeding the sepals, sharply carinate. Flowers subsessile. Sepals narrowly elliptic, obtuse, to 36 mm. long and 10 mm.

wide, submembranaceous, glabrous outside, punctulate-lepidote inside, free. Petals ligulate, acute, 7 cm. long, erect, blue. Stamens slightly exserted. Ovary slenderly conic.

Vera Cruz, British Honduras, Honduras, Costa Rica, Panama.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. ca. 1500–2000 m., Woodson, Allen & Seibert 992; Finca Lérída to Peña Blanca, alt. 1750–2000 m., Woodson & Schery 320; vicinity of Boquete, alt. 1200–1500 m., Woodson & Schery 806.

15. *TILLANDSIA FESTUCOIDES* Brongn. ex Mez in DC. Monogr. Phan. 9:678. 1896.
Tillandsia caricifolia E. Morr. ex Mez in DC. Monogr. Phan. 9:672. 1896.

Plant 20–55 cm. high. Leaves many in a dense fasciculate rosette, often ex-



Fig. 114. *Tillandsia festucoides*

ceeding the inflorescence, densely appressed-lepidote; sheaths narrowly subtriangular, conspicuous, castaneous or ferruginous; blades linear-subulate to filiform, green. Scape erect or ascending, usually slender. Scape-bracts densely imbricate, the lower foliaceous, the upper subelliptic, filiform-laminate, chartaceous, often bright red. Inflorescence densely digitate, subellipsoid or broadly pyramidal, to 17 cm. long. Primary bracts like the upper scape-bracts but the higher ones not laminate, at least their sheaths much shorter than the axillary branches. Branches arching-recurved, linear, 3–9 cm. long, complanate. Floral bracts barely imbricate, lance-ovate, acute, 17–22 mm. long, exceeding the sepals, carinate and often incurved, subcoriaceous, usually nerved, pale-appressed-lepidote to glabrous, green or red. Flowers subsessile. Sepals lanceolate, glabrous or sparsely lepidote, the posterior ones connate, 6–8 mm. long. Petals tubular-erect, 25–30 mm. long, purple. Stamens exserted. Capsule cylindric, 25–30 mm. long.

Florida, Greater Antilles, southern Mexico, Central America.

BOCAS DEL TORO: Pumpkin River, vicinity of Chiriquí Lagoon, von Wedel 2563.

16. *TILLANDSIA JUNCEA* (R. & P.) Poir. in Lam. Encycl. Suppl. 5:309. 1817.*Bonapartea juncea* R. & P. Fl. Peruv. 3:38. 1802.*Misandra juncea* (R. & P.) Dietr. Lex. Nachtr. 5:103. 1819.*Acanthospora juncea* (R. & P.) Spreng. Syst. 2:25. 1825.*Tillandsia quadrangularis* Mart. & Gal. in Bull. Acad. Brux. 10¹:119. 1843.*Platystachys juncea* (R. & P.) Beer, Bromel. 86. 1857.*Tillandsia juncifolia* Regel in Gartenfl. 23:321. 1874.

Plants 2–4 dm. high, often with scaly branching rhizomes. Leaves many in a dense fasciculate rosette, usually equaling the inflorescence or shorter, densely

subappressed-lepidote; sheaths triangular-ovate, conspicuous, ferruginous; blades linear-subulate, filiform-acuminate. Scape erect or ascending, stout. Scape-bracts densely imbricate, lance-elliptic, acuminate, filiform-laminate, subchartaceous, densely pale-lepidote. Inflorescence densely digitate from a few spikes or sometimes reduced to a single densely polystichous-flowered spike, ovoid, rarely over 7 cm. long. Primary bracts like the upper scape-bracts, subinvolute below the inflorescence, their sheaths slightly shorter than the lower axillary spikes, their blades mostly exceeding them. Spikes sessile, elliptic or lanceolate, acute, to 4 cm. long, stout, slightly complanate. Floral bracts densely imbricate, broadly ovate, exceeding the sepals, carinate in the distichous-flowered spikes, coriaceous or subcoriaceous, nearly or quite even, densely lepidote, often red. Flowers subsessile. Sepals lanceolate, acute, 15–20 mm. long, glabrous or sparsely



Fig. 115
Tillandsia juncea

lepidote, the posterior ones much connate. Petals tubular-erect, to 4 cm. long, violet. Stamens exserted. Capsule slenderly cylindric, 25–35 mm. long.

Florida, Cuba, Jamaica, Hispaniola, southern Mexico, Central America, Trinidad and Colombia south to Peru and Bolivia.

BOCAS DEL TORO: Water Valley, *von Wedel 648*. CHIRIQUÍ: pastures around El Boquete, alt. 1000–1300 m., *Pittier 3010*; valley of the Río Caldera, from El Boquete to the Cordillera, alt. 1400–1600 m., *Killip 3511*; Bajo Mono, Boquete District, alt. 1350 m., *Davidson 467*; Finca Lérica to Boquete, alt. ca. 1300–1700 m., *Woodson, Allen & Seibert 1128*.

17. *TILLANDSIA ACOSTAE* Mez & Tonduz in Fedde Rep. Spec. Nov. 14:252. 1916.

Plant 20–25 cm. high. Leaves many in a dense rosette, about equaling the inflorescence, rigid, densely and minutely appressed-lepidote; sheaths elliptic-oblong, 3–4 cm. long, dark castaneous; blades narrowly triangular, acuminate, 10–15 mm. wide, involute toward apex. Scape erect, short, stout. Scape-bracts densely imbricate, foliaceous, subinflated. Inflorescence simple or of 2 subequal sessile spikes.

Primary bracts like the upper scape-bracts but not laminate, scarcely longer than the floral bracts. Spikes linear, acuminate, terete, 7–14 cm. long, 2 cm. thick. Floral bracts densely imbricate, suborbicular, apiculate, 2 cm. long, exceeding the sepals, inflated, carinate toward apex, coriaceous, even, glabrous. Flowers subsessile. Sepals lanceolate, acute, 14 mm. long, the posterior ones much connate. Petals tubular-erect, 35 mm. long. Stamens exserted.

Costa Rica, Panama.

CHIRIQUÍ: vicinity of Puerto Armuelles, alt. 0–75 m., Woodson & Schery 823.

18. *TILLANDSIA BALBISIANA* Schult. in R. & S. Syst. Veg. 7:1212. 1830.

Platystachys digitata Beer, Bromel. 84. 1857.

Tillandsia Urbaniana Wittm. in Engler's Bot. Jahrb. 11:65. 1889.

Tillandsia cubensis Gandoger in Bull. Soc. Bot. France 66:290. 1920.



Fig. 116. *Tillandsia Balbisiana*

Plant stemless, 13–65 cm. high. Leaves many, densely and minutely pale-appressed-lepidote, often purple-margined; sheaths ovate, large, inflated, forming

an ovoid or ellipsoid pseudobulb to 12 cm. long, pale-ferruginous toward base; blades abruptly spreading or recurved from the apices of the sheaths, linear, filiform-acuminate, 1 cm. wide, usually all involute. Scape erect or ascending, slender, subglabrous. Scape-bracts imbricate, elliptic with long linear spreading or reflexed blades, inflated. Inflorescence densely pinnate or subdigitate or rarely simple, slenderly fusiform or subcylindric, to 2 dm. long. Primary bracts like the upper scape-bracts, at least their sheaths shorter than the axillary spikes. Spikes sessile, strict, linear, acute, complanate, 3–12 cm. long, 12 mm. wide. Floral bracts imbricate, ovate, obtuse and apiculate but often appearing acute, 15–22 mm. long, exceeding the sepals, coriaceous, even or slightly nerved toward apex, glabrous or obscurely lepidote, ecarinate, often bright red. Flowers subsessile. Sepals lanceolate, acute, glabrous, connate posteriorly. Petals tubular-erect, obtuse, 30–45 mm. long, violet. Stamens exserted. Capsule cylindric, 4 cm. long.

Florida, Bahamas, Cuba, Jamaica, Hispaniola, Sinaloa to Veracruz and south to Panama.

CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 29679*; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen 17036*; vicinity of Juan Mina, Chagres River, *Bartlett & Lasser 16814*.

19. *TILLANDSIA PUNCTULATA* Schlecht. & Cham. in *Linnaea* 6:53. 1831.



Fig. 117. *Tillandsia punctulata*

Tillandsia tricolor sensu E. Morr. in Belg. Hort. 29:162. 1879, non Schlecht. & Cham. 1831.

Tillandsia melanopus E. Morr. ex Mez in DC. Monogr. Phan. 9:680. 1896.

Plant 25–45 cm. high. Leaves many in a dense rosette, equaling or exceeding the inflorescence but usually recurved, densely and minutely appressed-lepidote; sheaths broadly ovate to elliptic-oblong, 4–8 cm. long, deep castaneous; blades narrowly triangular, filiform-acuminate but with blunt apex, 5–10 mm. wide. Scape erect. Scape-bracts foliaceous but red-brown, all linear-laminate, usually subinvolucrate below the inflorescence. Inflorescence simple and distichous-flowered or densely digitate from 2–5 spikes. Primary bracts like the scape-bracts but very short-laminate, less than half as long as the spikes. Spikes sessile, ovate or lanceolate, acute, slightly complanate, 7–10 cm. long, 25–35 mm. wide. Floral bracts densely imbricate, broadly ovate, acute, to 4 cm. long, exceeding the sepals, subinflated, carinate, coriaceous with broad membranous margin, nerved, minutely lepidote. Flowers subsessile. Sepals lance-oblong, acute, 30–35 mm. long, complicate, alate, densely and minutely lepidote. Petals tubular-erect, 4–6 cm. long, white near apex, violet below. Stamens exserted. Capsule cylindric, acute, 3 cm. long.

Southern Mexico, Central America, Surinam.

CHIRIQUÍ: 1883, *Pfau*; Volcán de Chiriquí, Boquete District, alt. 2100 m., *Davidson* 965; vicinity of Casita Alta, Volcán de Chiriquí, alt. ca. 1500–2000 m., *Woodson, Allen & Seibert* 991; vicinity of Finca Lérída, alt. 1750 m., *Woodson & Schery* 226.

20. *TILLANDSIA FASCICULATA* Sw. Prodr. 56. 1788.

Tillandsia fasciculata var. *latispica* Mez in DC. Monogr. Phan. 9:683. 1896.



Fig. 118. *Tillandsia fasciculata*

Plant 2–10 dm. high. Leaves rosulate; sheaths large, ovate, dark castaneous; blades narrowly triangular, 2–3 cm. wide, finely lepidote. Scape erect, stout. Scape-bracts imbricate, the lower ones foliaceous. Inflorescence simple or digitate. Primary bracts broadly ovate, acuminate, shorter than the spikes. Spikes sessile or subsessile, erect, bearing reduced sterile bracts at base, usually over 1 dm. long, strongly complanate. Floral bracts imbricate, broad, acute, 2–4 cm. long, carinate, nearly or quite even, coriaceous, glabrous or subglabrous. Sepals usually shorter than the bracts, the posterior ones connate. Petals 6 cm. long, white to purple. Stamens exserted.

Florida, West Indies, Mexico to Colombia and Guiana.

PANAMÁ: near the big swamp east of Río Tecúmen, *Standley 26697, 26702*. CANAL ZONE: Maumé and Gorgona, *Wagner*; Río Paraíso, above East Paraíso, *Standley 29860*; Barro Colorado Island, *Kenoyer 211*; near Madden Dam and along Azote Caballo Road near Alahueta, alt. 90–100 m., *Dodge 16589*; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen 16589a*.

TILLANDSIA FASCICULATA var. *CONVEXISPICA* Mez in DC. Monogr. Phan. 9:683. 1896.

Spikes to 2 dm. long, only slightly complanate. Floral bracts large, even or faintly nerved.

Jamaica, Mexico, British Honduras, Guatemala, Panama.

CANAL ZONE: Barro Colorado Island, *Chickering 63*.

TILLANDSIA FASCICULATA var. *UNCISPICA* Mez in DC. Monogr. Phan. 9:684. 1896.

Inflorescence few-branched. Spikes short-stipitate, narrow, dense, mostly less than 1 dm. long. Floral bracts less than 25 mm. long, incurved.

Cuba, Santo Domingo, Saint Lucia, Guatemala, Panama.

BOCAS DEL TORO: Isla Colón, *von Wedel 118*; Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 1377, 1396*; Little Bocas, vicinity of Chiriquí Lagoon, *von Wedel 2528*.

21. *TILLANDSIA MELANOCRATER* L. B. Smith in Contrib. Gray Herb. 117:31. 1937.

Tillandsia melanopus E. Morr. ex Mez in DC. Monogr. Phan. 9:680. 1896, in part, not as to type.

Plant rarely over 25 cm. high, often propagating by scaly branching rhizomes. Leaves very numerous in a subspreading rosette, 15–20 cm. long, densely and finely appressed-lepidote; sheaths broadly ovate, deep castaneous, blades curved, linear-triangular, long-acuminate, pungent, 8 mm. wide, flat. Scape erect or ascending, slender. Scape-bracts densely imbricate, broadly ovate, lepidote, at least the lower ones with a linear blade. Inflorescence simple or digitate from a few spikes. Primary bracts like the upper scape-bracts, scarcely longer than the floral bracts. Spikes variable, from narrowly oblong and acute to broadly elliptic and obtuse, 4–9 cm. long, 12–20 mm. wide, complanate with flat sides, often bearing several reduced sterile bracts toward base. Rhachis slender, nearly straight. Floral bracts imbricate but not always concealing the rhachis, ovate, 20–25 mm. long, exceeding

the sepals, carinate, coriaceous, even, glabrous or toward apex sparsely lepidote. Flowers subsessile. Sepals lanceolate, acute, 15–19 mm. long, much connate posteriorly. Petals tubular-erect, 30–35 mm. long, violet. Stamens exserted. Capsule slenderly cylindric, 3 cm. long.

Guatemala, Costa Rica, Panama.

CHIRIQUÍ: forests around El Boquete, alt. 1000–1300 m., *Pittier 2987*; Finca Lérica to Boquete, alt. ca. 1300–1700 m., *Woodson, Allen & Seibert 1129*; vicinity of El Boquete, alt. 1200–1500 m., *Woodson & Schery 807, 808*. COLÓN: forests around Porto Bello, alt. 5–100 m., *Pittier 2473*. CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 29561*; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen 17033*; drowned forest of Quebrada Ancha, alt. 70 m., *Dodge & Steyermark 17033a*.



Fig. 119
Tillandsia
subulifera

22. *TILLANDSIA SUBULIFERA* Mez in Fedde Rep. Spec. Nov. 16:74. 1919.

Plant 15–19 cm. high. Leaves few in a distinct but slenderly cylindric pseudobulb, erect, the inner ones to 18 cm. long, the outer greatly reduced, appressed-canescens-lepidote, concolorous or with faint white cross-bands; sheaths about half as long as the blades, ample; blades linear, abruptly acute or obtuse, 5 mm. wide, complicate, angled. Scape erect, slender, largely concealed by the leaves. Scape-bracts imbricate, nerved, densely lepidote. Inflorescence simple, oblong or linear, 5–7 cm. long, distichously 4- to 6-flowered. Axis slender, geniculate, mostly exposed, appressed-lepidote. Floral bracts erect, elliptic, broadly acute, 2 cm. long, shorter than the sepals, incurved and somewhat carinate toward apex, nerved, appressed-lepidote. Flowers short-pedicellate. Sepals free, elliptic, narrowly obtuse, 22 mm. long, nerved, lepidote. Petals tubular-erect, 32 mm. long, yellow or white when dry. Stamens exserted. Capsule slenderly cylindric, 6 cm. long.

Trinidad, Panama.

CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 20664*; Barro Colorado Island, *Chickering 62*; *Shattuck 1166*.

23. *TILLANDSIA BUTZII* Mez in Engler, Pflanzenreich 4: Fam. 32:636. 1935.

Tillandsia variegata Schlecht. in Linnaea 18:429. 1844, non Vell. 1827.

Plant 2–3 dm. high. Leaves few in a bulbous rosette, to 5 dm. long, densely and finely pale-appressed-lepidote throughout, the margins at first ciliate with coarse scales; sheaths suborbicular, inflated, forming a pseudobulb 25–45 mm. thick, dark brown or purple with many large pale green often confluent spots; blades involute-subulate, filiform-acuminate, 3 mm. thick, contorted. Scape erect, slender. Scape-bracts foliaceous, imbricate. Inflorescence digitate from a few subequal spikes or rarely simple. Primary bracts subfoliaceous, concolorous, the broadly ovate sheath much shorter than the axillary spike, the linear blade often

much exceeding it. Spikes erect to spreading, linear, acute, complanate, 6–8 cm. long, about 1 cm. wide, 5- to 8-flowered with 1–2 sterile bracts at base. Floral bracts erect, imbricate, ovate, acute, 20–28 mm. long, much exceeding the sepals, subcoriaceous, densely lepidote, nerved. Flowers subsessile. Sepals narrowly elliptic, obtuse, 12–15 mm. long, glabrous. Petals tubular-erect, 30–35 mm. long, violet. Stamens exserted. Capsule slenderly cylindric, 3 cm. long.

Southern Mexico, Central America.

CHIRIQUÍ: pastures around El Boquete, alt. 1000–1300 m., *Pittier 3011*; trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt. 1500–2000 m., *Allen 1592*.

24. *TILLANDSIA BULBOSA* Hook. Exot. Fl. *pl.* 173. 1826.

Tillandsia bulbosa var. *brasiliensis* Schultes in R. & S. Syst. Veg. 7:1212. 1830.

Tillandsia bulbosa var. *picta* Hook. in Bot. Mag. *pl.* 4288. 1847.

Tillandsia inanis Lindl. & Paxt. Fl. Gard. 1:159. 1850.

Tillandsia erythraea and *T. pumila* Lindl. & Paxt. Fl. Gard. 1:160. 1850.

Platystachys inanis (Lindl.) Beer, Bromel. 82. 1857.

Platystachys bulbosa (Hook.) and *P. erythraea* (Lindl.) Beer, Bromel. 83. 1857.

Plants usually in dense masses, 7–22 cm. high. Leaves 8–15, often exceeding the inflorescence, covered with fine appressed cinereous scales; sheaths orbicular, abruptly contracted into the blades, much inflated, 2–5 cm. long, forming a dense ovoid pseudobulb, green or greenish white, often with a narrow red or purple margin; blades involute-subulate, acuminate, contorted, spreading, to 3 dm. long, 2–7 mm. thick. Scape erect. Scape-bracts with elongate foliaceous blades exceeding the inflorescence, the upper ones often red. Inflorescence simple or subdigitate from a few spikes, red or green. Primary bracts ovate, acute, much shorter than the spikes but their foliaceous blades sometimes exceeding them. Spikes spreading, lanceolate, acute, complanate, 2–5 cm. long, 2- to 8-flowered. Rhachis slender, lepidote. Floral bracts erect, imbricate, ovate, acute, 15 mm. long, exceeding the sepals, carinate, subchartaceous, lepidote. Flowers sessile. Sepals oblong, apiculate, 13 mm. long, the posterior ones somewhat connate. Petals 3–4 cm. long, blue or violet. Stamens exserted. Capsule cylindric, to 4 cm. long.

Southern Mexico, Central America, West Indies, Trinidad, Colombia, Venezuela, Guiana, Brazil.

BOCAS DEL TORO: Isla Colón, vicinity of Chiriquí Lagoon, *von Wedel 130, 1330*; Water Valley, *von Wedel 646*; Little Bocas, vicinity of Chiriquí Lagoon, *von Wedel 2537*; Darkland, vicinity of Chiriquí Lagoon, *von Wedel 2622*. COCLÉ: vicinity of Penonomé, *Williams 609*. CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 25754, 29665, 29690*; Balboa, *Standley 28569*; Brazos Brook Reservoir, *Stevens 717*; Barro Colorado Island, *Standley 40878, Aviles 27, Bailey 371, Shattuck 154, 521*; near Madden Dam and along Azote Caballo Road near Alahuela, alt. 90–100 m., *Dodge 16581*; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen 16581a*. INDEFINITE: *Cowell 412*.

25. *TILLANDSIA INCURVA* Griseb. in Nachr. Ges. Wiss. Gött. 1864:15. 1865.

Tillandsia digitata Mez in DC. Monogr. Phan. 9:715. 1896.

Tillandsia castaneo-bulbosa Mez & Wercklé in Bull. Herb. Boiss. II. 3:140. 1903.

Plant 15–40 cm. long with the inflorescence extended. Leaves many in a dense subbulbous rosette, 15–35 cm. long, very densely and finely appressed-lepidote throughout; sheaths large, distinct, broadly ovate to suborbicular, dark castaneous; blades narrowly triangular, long-acuminate, 2–3 cm. wide, cinereous-lepidote. Scape arching-decurved, slender, short. Scape-bracts barely imbricate, involute, obovate or elliptic, densely lepidote, at least the lower ones caudate. Inflorescence simple or digitate with 2–5 spikes. Primary bracts like the scape-bracts, scarcely larger than the floral bracts. Spikes strict, linear or lance-linear with several sterile bracts at base, acute, 10–24 cm. long, complanate, 7- to 16-flowered. Rhachis flexuous, slender, angled, excavated next the flowers, lepidote at first. Floral bracts erect or slightly divergent, two to three times as long as the internodes but usually exposing most of the rhachis, elliptic, obtuse, 25–35 mm. long, much exceeding the sepals, ecarinate at maturity, red, submembranaceous, nerved to almost even, appressed-lepidote to glabrous. Flowers distinctly pedicellate. Sepals free, elliptic, obtuse or apiculate, 15–20 mm. long, soon glabrous, stramineous. Petals 35 mm. long, yellow. Stamens exerted.

Southern Florida, Cuba, Jamaica, Costa Rica, Panama, Venezuela, Colombia, Bolivia.

CHIRIQUÍ: vicinity of Finca Lérica, alt. 1750 m., *Woodson & Schery* 223.

26. *TILLANDSIA VALENZUELANA* A. Rich. in Sagra, Hist. Cuba 11:267. 1850.

Tillandsia laxa Griseb. Fl. Brit. W. Ind. 596. 1864.

Tillandsia Kunthiana sensu Griseb. in Nachr. Ges. Wiss. Gött. 1864:15. 1865, non Gaud. 1846.

Tillandsia brachypoda Baker in Jour. Bot. 25:237. 1887.

Tillandsia sublaxa Baker in Jour. Bot. 25:280. 1887.

Tillandsia polystachya var. *alba* Wittm. in Engler's Bot. Jahrb. 11:65. 1889.

Tillandsia Purpusii Mez in Fedde, Rep. Spec. Nov. 14:251. 1916, in part.

Tillandsia domingensis Mez in Fedde, Rep. Spec. Nov. 16:73. 1919.

Plant 2–6 dm. high. Leaves many in a utriculate rosette, to 4 dm. long, the outer reduced to scale-like sheaths, very densely and finely appressed-cinereous-lepidote throughout, sometimes becoming glabrous above; sheaths large, ovate, concolorous with the blade; blades linear-triangular, acuminate, usually flat, 10–25 mm. wide. Scape central, erect or ascending, slender, glabrous. Scape-bracts imbricate, ovate, inflated, cinereous-lepidote, pink or red, fading to olivaceous, at least the lower ones with linear foliaceous blades. Inflorescence simple or pinately compound from a few spikes. Axes slender, soon glabrous. Primary bracts like the upper scape-bracts, their sheaths much shorter than the spikes but their blades sometimes exceeding the lower ones. Spikes divergent, oblong, acute, complanate, often rather lax, 6- to 17-flowered, especially the terminal spike with sterile bracts at base, 5–20 cm. long, 1–2 cm. wide. Rhachis angled, slightly flexuous. Floral bracts erect or suberect, usually 2–3 times as long as the internodes but exposing the rhachis, elliptic-oblong, obtuse or apiculate, 2 cm. long, much exceeding the sepals, submembranaceous, nerved, subglabrous, pink or red,

sometimes carinate toward apex. Flowers subsessile. Sepals oblong, obtuse, somewhat connate posteriorly. Petals linear, 3 cm. long, lilac or violet. Stamens exserted. Capsule prismatic, 3 cm. long.

Southern Florida, Greater Antilles, southern Mexico, Central America, Colombia, Venezuela, Bolivia.

BOCAS DEL TORO: Water Valley, *von Wedel* 739, 1395, 1557. CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley* 29562, 29667; near Madden Dam and along Azote Caballo Road near Alahuela, alt. 90-100 m., *Dodge*.

27. *TILLANDSIA KEGELIANA* Mez in DC. Monogr. Phan. 9:725. 1896.

Leaves many in a dense rosette, 12-17 cm. long; sheaths broadly ovate, over 3 cm. long, thin, castaneous-lepidote; blades often secund, involute-subulate, acuminate, 5 mm. wide, rigid, densely pale-lepidote. Scape slender, ascending, very short, glabrous. Scape-bracts densely imbricate, lance-ovate, long-caudate, appressed-lepidote. Inflorescence simple, exceeded by the leaves, densely 6- to 8-flowered, elliptic in outline, strongly complanate, 40-55 mm. long, 30-35 mm. wide. Rhachis undulate, angled, glabrous. Floral bracts suberect, densely im-



Fig. 120. *Tillandsia Kegeliana*

bricate, acuminate from a broadly elliptic base, incurved, 3 cm. long, 16 mm. wide, fleshy, bright red when fresh, minutely rugulose and blackish when dry, glabrous. Flowers erect or suberect. Pedicels short and thick. Sepals free, elliptic, obtuse, 2 cm. long, coriaceous when dry, densely punctulate-lepidote, slightly nerved. Petals over 4 cm. long, dark purple. Stamens exserted. Capsule subprismatic, over 5 cm. long.

Panama, Colombia, Surinam.

DARIÉN: forests around Yaviza, southern Darién, *Pittier* 6583.

3. *VRIESIA* Lindl.

VRIESIA Lindl. in Bot. Reg. 29: pl. 10. 1843. *Nomen conservandum*, non *VRIESIA* Hassk. 1842.

Hexalepis Raf. Fl. Tellur. 4:24. 1838.

Vriesia subgenus *Alcantarea* E. Morr. ex Mez in Mart. Fl. Bras. 3³:516. 1894.

Neovriesia Britton in Britton & Wilson, Sci. Surv. Porto Rico 5:141. 1923.

Alcantarea Harms in Notizbl. Bot. Gart. Berlin 10:802. 1929.

Large showy mostly epiphytic herbs. Leaves densely rosulate, often banded or mottled, entire. Inflorescence simple or compound, spikes usually distichous-flowered. Floral bracts conspicuous, enfolding or concealing the bases of the flowers. Flowers subsessile or on short pedicels. Sepals free. Petals nearly or quite free, ligulate, bearing one or two scales each. Stamens included or exerted. Ovary nearly or quite superior; style elongate. Ovules many, usually caudate. Seeds fusiform with a long straight basal coma.

- a. Flowers not becoming secund at anthesis.
 - b. Floral bracts shorter than the sepals; inflorescence compound..... 1. *V. ALTA*
 - bb. Floral bracts equaling or exceeding the sepals; inflorescence simple.
 - c. Floral bracts chartaceous, sharply carinate, strongly incurved toward apex..... 2. *V. HELICONTIODES*
 - cc. Floral bracts coriaceous, convex and ecarinate, straight.
 - d. Leaves acute, not apiculate; floral bracts barely imbricate..... 3. *V. PACHYSPATHA*
 - dd. Leaves broadly acute or obtuse, apiculate; floral bracts densely imbricate..... 4. *V. GLADIOLIFLORA*
- aa. Flowers becoming secund at anthesis.
 - b. Floral bracts acute or obtuse; axis of the inflorescence smooth or sulcate but never verrucose.
 - c. Floral bracts rugulose when dry, thick, coriaceous.
 - d. Sepals obtuse; floral bracts obtuse or broadly subacute 4. *V. GLADIOLIFLORA*
 - dd. Sepals acute; floral bracts triangular-acute..... 5. *V. WOODSONIANA*
 - cc. Floral bracts not rugulose when dry.
 - d. Plant 1-2 m. high; leaf-blades 8-10 cm. wide; floral bracts coriaceous..... 6. *V. SANGUINOLENTA*
 - dd. Plant not over 5 dm. high; leaf-blades 13-18 mm. wide; floral bracts chartaceous..... 7. *V. SUBSECUNDA*
 - bb. Floral bracts acuminate, carinate toward apex; axis of the inflorescence verrucose just below the nodes 8. *V. RINGENS*

1. *VRIESIA ALTA* (Baker) E. Morr. ex Mez in DC. Monogr. Phan. 9:617. 1896.

Tillandsia alta Baker, Handb. Bromel. 226. 1889.



Fig. 121
Vriesia alta

Flowering plant about 2 m. high. Leaves 1 m. long, nearly 1 dm. wide, acuminate, usually incurved at apex, marked with dark purple at base. Scape very stout. Scape-bracts exceeding the internodes, subspreading, dark purple at base and green at apex. Inflorescence amply paniculate, about 1 m. long. Branches suberect, 2-6 dm. long, 10- to 15-flowered. Floral bracts ovate to suborbicular, broadly obtuse, 37 mm. long, much exceeded by the sepals, carinate but not incurved, pale green with brownish purple markings. Flowers divergent to spreading, not secund, to 125 mm. long. Pedicels very thick, 6 mm. long. Sepals elliptic, obtuse, 41 mm. long, 21 mm. wide, purple-bordered, carinate especially toward base. Petals fasciate, at first white, then yellow and finally dull red.

Jamaica, Panama.

CHIRIQUÍ: in Panama known only from material cultivated at Liège, Belgium.

2. *VRIESIA HELICONIODES* (HBK.) ex Walp. Ann. Bot. 3:623. 1852.

Tillandsia heliconioides HBK. Nov. Gen. & Sp. 1:293. 1816.

Tillandsia disticha Willd. ex Schultes in R. & S. Syst. Veg. 7:1226. 1830, in synon.

Platystachys disticha (Willd.) Beer, Bromel. 264. 1857.

Vriesia Falkenbergii Bull in Gard. Chron. II. 13:759. 1880.

Vriesia bellula Linden, Cat. 109:7. 1883.

Vriesia disticha O. Ktze. Rev. Gen. 3:304. 1898, in part, as to material cited.

Guzmania obtusata Rusby in Mem. N. Y. Bot. Gard. 7:212. 1927.

Rarely over 4 dm. high. Leaves about 2 dm. long, green above, suffused with red and sometimes spotted below; sheaths distinct, obscurely punctulate-lepidote; blades ligulate, acute or acuminate, 15–30 mm. wide, subglabrous. Scape erect, usually much shorter than the leaves. Scape-bracts densely imbricate, broadly ovate, acute. Inflorescence simple, distichous, oblong in outline, dense, 6- to 18-flowered, to 20 cm. long, 6 cm. wide, strongly complanate. Floral bracts broadly ovate and triangular-acute or subrhombic, to 45 mm. long, chartaceous, sharply carinate with the keel sigmoid in outline, bright red above the middle, greenish yellow at apex and margins. Flowers erect or suberect, subsessile, 6 cm. long. Sepals lanceolate, acuminate, 27 mm. long, thin. Petals white, linear, acute, bearing 2 ovate obtuse scales. Stamens included. Capsule 5 cm. long. Coma reddish brown.

Guatemala to Bolivia and southwestern Brazil.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1131*. CANAL ZONE: Caño Quebrado, *Pittier 6670*; Las Cascadas Plantation, near Summit, *Standley 29668*; vicinity of Las Cruces, alt. 26–40 m., *Seibert 575*; Río Chilibre, tributary of Chagres River, between Juan Mina and Madden Dam, *Bartlett & Lasser 16421*; Forest Reserve, near crossing of Cruces Trail and Madden Dam Road, *Bartlett & Lasser 16457*.



Fig. 122
Vriesia
pachyspatha

3. *VRIESIA PACHYSPATHA* Mez & Wercklé in Bull. Herb. Boiss. II. 4:867. 1904.

Flowering plant 5 dm. high, very stout. Leaves 10–15 in a dense rosette, 4 dm. long; blades 3 cm. wide, linear, acute, concolorous, subglabrous at maturity, coriaceous and rigid when dry. Scape erect, very stout. Scape-bracts foliaceous, strict, densely imbricate. Inflorescence simple, 20 cm. long, 75 mm. wide, rather laxly few-flowered, strongly compressed. Floral bracts barely imbricate, suborbicular or broadly ovate, broadly acute, about 6 cm. long, much exceeding the sepals, thick, coriaceous, straight, ecarinate, under a lens punctulate and transversely rugose. Flowers erect, not secund. Pedicels very short and stout. Sepals broadly elliptic, narrowly obtuse, 37 mm. long, 19 mm. wide, very thick, punctulate-lepidote, even or toward apex faintly striate.

Costa Rica, Panama.

CHIRIQUÍ: vicinity of Bajo Chorro, alt. 1900 m., *Woodson & Schery 679*.

4. *VRIESIA GLADIOLIFLORA* (Wendl.) Ant. in Wiener Ill. Gart.-Zeit. 5:97. 1880.*Tillandsia gladioliflora* Wendl. in Hamb. Gartenz. 19:31. 1863.*Vriesia gladioliflora purpurascens* Ant. in Wiener Ill. Gart.-Zeit. 5:97, pl. 1. 1880.*Vriesia princeps* Hort. Linden ex Batal. in Gartenfl. 26:158. 1877; cf. E. Morr. in Belg. Hort. 30:216. 1880.*Vriesia gladioliflora* var. *purpurascens* Ant. Phyto-Iconogr. 23. 1884, in synonym.

Fig. 123
Vriesia
gladioliflora

Plant up to 1 m. Leaves purplish when young, becoming deep green especially above; sheaths elliptic, inconspicuous, densely lepidote with brown punctiform scales; blades ligulate, broadly acute or obtuse, apiculate, 6–8 cm. wide, glabrous above, obscurely punctulate-lepidote beneath. Scape erect, very stout. Scape-bracts imbricate, elliptic, abruptly acute. Inflorescence simple, densely many-flowered, subcylindric at anthesis, acute, 2–4 dm. long, up to 5 cm. wide. Floral bracts distichous, erect, imbricate, broadly ovate, obtuse or broadly subacute, 45–55 mm. long, ecarinate, equaling to much exceeding the sepals, three to four times as long as the internodes, coriaceous, glabrous, green, purplish toward apex, becoming buff and finely rugulose when dry. Flowers slightly or not at all secund. Pedicels short and stout. Sepals broadly elliptic, obtuse, 20–45 mm. long, coriaceous. Petals ligulate with sub-orbicular blade, 4–7 cm. long, bearing 2 obovate subincised scales at base. Stamens and pistil shorter than the petals.

British Honduras, Guatemala, Costa Rica, Panama, Colombia.

CANAL ZONE: Barro Colorado Island, *Shattuck* 524; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen* 17037.

5. *VRIESIA WOODSONIANA* L. B. Smith in Woodson & Seibert in Ann. Missouri Bot. Gard. 26:275, pl. 20. 1939.

Leaves rosulate, up to 5 dm. long; sheaths elliptic, castaneous toward base, densely punctate-lepidote; blades ligulate, 3 cm. broad, flat, rounded at apex and apiculate, concolorous, densely and minutely lepidote beneath, glabrous above. Scape erect, glabrous. Scape-bracts foliaceous, densely imbricate. Inflorescence simple, curved, rather densely few-flowered, about 15 cm. long. Floral bracts imbricate, slightly secund, broadly ovate, triangular-acute, up to 45 mm. long and 33 mm. wide, exceeding the sepals, glabrous, strongly rugose when dry, not at all carinate, dark castaneous toward base. Flowers strongly secund. Pedicels 1 cm. long, very thick. Sepals broadly ovate, acute, 35–40 mm. long, rather thin, impressed-punctulate, rugulose when dry. Petals imperfectly known, at base bearing 2 scales 1 cm. long. Stamens apparently included.

Endemic.

CHIRIQUÍ: Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. ca. 1500–2000 m., *Woodson, Allen & Seibert* 1029.

6. *VRIESIA SANGUINOLENTA* Cogn. & Marchal, Pl. Ornem. pl. 52. 1874.*Tillandsia sanguinolenta* (Cogn. & Marchal) Baker, Handb. Bromel. 226. 1889.*Tillandsia ingens* Mez in Urb. Symb. Ant. 2:256. 1900.*Vriesea Alfarovii* Mez in Fedde Rep. Spec. Nov. 14:247. 1916.*Vriesea Urbaniana* Harms in Notizbl. 12:532. 1935.

Flowering plant 1-2 m. high. Leaves about 10 in a dense rosette, suberect, 6-7 dm. long, green, usually with large irregular spots of deep red especially near the base, obscurely punctulate-lepidote; sheaths ovate-elliptic, the same color as



Fig. 124

Vriesea sanguinolenta

the blades and but slightly broader; blades ligulate, acute or subrounded with a long apiculus, 8-10 cm. wide. Scape erect, much exceeding the leaves, over 1 cm. thick at summit, glabrous. Scape-bracts imbricate, broadly ovate, acute or the lower ones triangular-laminate, glabrous, even, thick, coriaceous. Inflorescence simple or few-branched, up to 4 dm. long. Primary bracts like the upper scape-bracts, covering only the sterile bases of the branches. Branches suberect, secundly 11- to 15-flowered, the lateral ones 25 cm. long with 1 or 2 sterile bracts at base, the terminal one nearly 4 dm. long with a sterile base as long as the fertile and appearing like a continuation of the scape. Rhachis up to 10 mm. thick, flexuous, strongly 4-angled, glabrous, dark, its internodes narrowly obconical. Floral bracts becoming secund with the flowers, broadly elliptic to suborbicular, abruptly acute, to 5 cm. long, some and usually all more than twice as long as the internodes, glabrous, even, rigid, coriaceous, green, drying to light

brown, incurved and carinate toward apex. Flowers spreading and downwardly secund. Pedicels very stout, up to 12 mm. long. Sepals broadly elliptic or ovate, obtuse or broadly acute, 30-45 mm. long, rigid, glabrous outside. Petals white, slightly exceeding the sepals, bearing 2 scales at base.

Cuba, Jamaica, Costa Rica, Panama, Colombia.

BOCAS DEL TORO: indefinite, von Wedel 473; Nueces Cay, vicinity of Chiriquí Lagoon, von Wedel 2934. PANAMÁ: top of peak among rocks, hills northeast of Hacienda La Joya, alt. 50-300 m., Dodge, Hunter, Steyermark & Allen 16907. CANAL ZONE: westerly arm of Quebrada Salamanca, alt. 70 m., Dodge, Steyermark & Allen 17038.

7. *VRIESIA SUBSECUNDA* Wittm. in Engler's Bot. Jahrb. 11:69. 1889.*Tillandsia subsecunda* (Wittm.) Baker, Handb. Brom. 217. 1889.*Vriesea diminuta* Mez & Wercklé in Bull. Herb. Boiss. II, 4:869. 1904.

Not over 5 dm. high. Leaves 20-35 cm. long, chartaceous, densely appressed-lepidote, brownish green, sometimes tinged with red or violet; blades linear, acuminate, 13-18 mm. wide. Scape slender, erect, usually exceeding the leaves. Scape-bracts imbricate, ovate or elliptic, acuminate or the upper acute, brown, submembranaceous. Inflorescence simple, densely 4- to 9-flowered, 4-9 cm. long.

Rhachis slender, flexuous, slightly angled. Floral bracts becoming secund with the flowers, broadly ovate, 26–30 mm. long, equaling the sepals at anthesis, convex, ecarinate, incurved toward apex, even, chartaceous, light brown, slightly lustrous. Flowers suberect, 28 mm. long. Pedicels very stout, 4 mm. long. Sepals elliptic, rounded and apiculate, 22 mm. long, 10 mm. wide, thin, even or nerved, glabrous outside. Petals yellow, each bearing 2 lanceolate scales near base. Stamens and pistil included.

Costa Rica, Panama.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 229*.

8. *VRIESIA RINGENS* (Griseb.) Harms in Notizbl. 10:801. 1929.

Tillandsia ringens Griseb. Cat. Pl. Cub. 255. 1866.

Tillandsia chagresiana Baker in Jour. Bot. 26:109. 1888.

Tillandsia Veitchii Baker, Handb. Bromel. 223. 1889.

Vriesia Veitchii E. Morr. ex Baker, l. c., nomen, in synonym.

Vriesia paniculata Mez in DC. Monogr. Phan. 9:614. 1896, as *V. paniculata*, quoad *Tillandsia ringens* Griseb., non quoad *T. paniculata* L.

Very variable in size. Leaves to 9 dm. long; sheaths ovate-elliptic, mostly indistinct, brown-punctulate-lepidote; blades ligulate, acute or acuminate, 6 cm. wide, green or occasionally with a faint purplish tinge, concolorous or obscurely banded, obscurely punctulate-lepidote beneath. Scape erect, stout. Scape-bracts densely imbricate, lance-elliptic, acute, pale green. Inflorescence laxly compound or rarely simple, up to 5 dm. long. Primary bracts like the scape-bracts but thinner, much shorter than the branches. Branches suberect, secondly few-flowered, bearing several imbricate sterile bracts at base. Rhachis usually slender, verrucose just below the nodes. Floral bracts broadly ovate, acuminate, 30–65 mm. long, enfolding the flowers, exceeding the sepals of at least the lower flowers, straight, carinate toward apex, green or brownish. Flowers erect, to 8 cm. long, glabrous. Sepals elliptic, acuminate, 25–35 mm. long, 13 mm. wide, subcoriaceous, lustrous. Petals white or yellow, coiling-recurved, shorter than the stamens, flaccid, bearing 2 large spatulate acute scales at base.

West Indies, Costa Rica, Panama, Colombia.

COLÓN: Chagres, *Fendler 448*. CANAL ZONE: westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen*. DARIÉN: rain forest, Cana-Cuasi Trail, Chepigana District, alt. 1350 m., *Terry 1527*.



Fig. 125
Vriesia ringens

4. THECOPHYLLUM André

THECOPHYLLUM André, *Bromel. Andr.* 107. 1889; emend Mez in *Bull. Herb. Boiss.* II. 3:131. 1903.

Guzmania subgenus *Thecophyllum* (André) Mez in DC. *Monogr. Phan.* 9:915. 1896.

Acaulescent or rarely caulescent, mostly epiphytic. Leaves entire, often conspicuously marked. Inflorescence always compound though often very depauperate, spikes with flowers polystichous or reduced to a single perfect flower, but the presence of both primary and floral bracts indicating a compound inflorescence. Branches usually aborted. Floral bracts relatively inconspicuous. Flowers perfect. Sepals free in all species of Panama. Petals free, bearing 2 scales near the base. Stamens free, included. Pistil included; style filiform.

- a. Branches of the inflorescence nearly or quite aborted, with the flowers fascicled or solitary in the axils of the primary bracts.
 - b. Perfect flowers solitary in the axil of each primary bract but the floral bracts indicating a compound inflorescence..... 1. *T. INSIGNE*
 - bb. Perfect flowers 2 in the axil of each primary bract.
 - c. Leaf-blades marked with fine wavy transverse lines..... 2. *T. IRAZUENSE*
 - cc. Leaf-blades concolorous.
 - d. Inflorescence pendulous; primary bracts yellow and scarlet; floral bracts coriaceous..... 3. *T. ORORIENSE*
 - dd. Inflorescence erect; primary bracts green; floral bracts membranaceous..... 4. *T. ACUMINATUM*
- aa. Branches of the inflorescence developed.
 - b. Flowers on slender pedicels 1-2 cm. long..... 5. *T. PEDICELLATUM*
 - bb. Flowers sessile or subsessile..... 6. *T. CRASSIFLORUM*

1. *THECOPHYLLUM INSIGNE* (Mez) Mez in *Bull. Herb. Boiss.* II. 3:131. 1903.

Guzmania insignis Mez in DC. *Monogr. Phan.* 9:916. 1896.



Fig. 126
Thecophyllum insigne

Long-caulescent with the flowering scape 12 cm. high, the stem 3-4 dm. in addition, simple or branched, 6 mm. thick. Leaves densely imbricate along the stem, 1-2 dm. long, fimbriate-lepidote on the margin; sheaths 3 cm. long, broad, dark castaneous; blades linear, acuminate, not over 5 mm. wide, flat, green, soon glabrous. Scape erect, very slender, distinguished from the stem only by the coloration of its bracts. Scape-bracts imbricate, bright red, lanceolate with an elongate linear-acuminate green blade. Inflorescence laxly few-flowered, 4-9 cm. long, glabrous. Primary bracts like the scape-bracts but at least the upper ones wholly red, exceeding the sepals. Branches 1-flowered, slender, 2-3 mm. long, about as long as the pedicels and distinguished from them only by the position of the floral bracts. Floral bracts 2 on each branch, one sometimes bearing a much-reduced sterile flower, elliptic, obtuse, 5 mm.

long, thin. Flowers usually secund. Sepals elliptic, obtuse, 8–9 mm. long, free, coriaceous, red. Petals obovate, obtuse, 13–15 mm. long, dark purple. Stamens and pistil included. Capsule ovoid, acute, short.

Costa Rica, Panama.

CHIRIQUÍ: Mount Chiriquí, *Pfau* 229. COCLÉ: north of El Valle de Anton, trail to Las Minas, alt. ca. 1000 m., *Allen* 2885.

2. *THECOPHYLLUM IRAZUENSE* Mez & Wercklé in Bull. Herb. Boiss. II. 3:138. 1903.

Stemless, 7–10 dm. or higher. Leaves many, rosulate, erect, up to 4 dm. long; sheaths large, densely and minutely pale-lepidote, dark red-brown at base; blades subgligate, acute, 4–7 cm. wide, reddish violet, very densely marked with faint wavy transverse lines, apex recurved. Scape stout, glabrous. Scape-bracts erect, involute, exceeding the internodes, ovate-elliptic, caudate, subinflated. Inflorescence dense, slenderly cylindric, 15–30 cm. long, 4–6 cm. thick, glabrous. Primary bracts reflexed with spirally revolute apex, like the scape-bracts, the lower ones longer than the flowers. Branches very short or wholly aborted. Floral bracts suborbicular or reniform, 8–15 mm. long, obtuse, scarcely carinate, thin. Flowers 2 in each axil. Sepals broadly elliptic, 15–20 mm. long, 10–15 mm. wide, thick, coriaceous, free.

Costa Rica, Panama.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, alt. 1800 m., *Davidson* 281.

3. *THECOPHYLLUM ORORIENSE* (Mez) Mez in Bull. Herb. Boiss. II. 3:131. 1903. *Guzmania Orioriensis* Mez in DC. Monogr. Phan. 9:917. 1896.

Stemless, 5–8 dm. high. Leaves many, suberect, densely rosulate, 35–55 cm. long; sheaths large, ovate, castaneous; blades subobtruse and apiculate, 5–6 cm. wide, soon glabrous above, punctulate beneath with brownish purple scales. Scape decurved, very stout, equaling or longer than the leaves. Scape-bracts exceeding the internodes, very broadly ovate with a triangular acute blade, recurved or spirally involute toward the apex or rarely suberect, subinflated. Inflorescence many-flowered, densely cylindric especially toward apex, up to 2 dm. long, 65 mm. in diameter, glabrous. Primary bracts broadly triangular-ovate, exceeding the 2 flowers in each axil, recurved, yellow at base, bright scarlet toward apex. Branches almost wholly aborted. Floral bracts suborbicular, 12 mm. long, exceeded by the sepals, carinate, coriaceous, thick. Pedicels short and thick. Sepals obovate, 20 mm. long, 15 mm. wide, free. Petals 3 cm. long, yellow, bearing 2 large acuminate scales at base. Stamens included.



Fig. 127

Thecophyllum ororiense

Costa Rica, Panama.

CHIRIQUÍ: Finca Lérída to Peña Blanca, alt. 1750–2000 m., *Woodson & Schery 321*.

4. *THECOPHYLLUM ACUMINATUM* L. B. Smith in *Contrib. Gray Herb.* 117:30. 1937.



Fig. 128
Thecophyllum
acuminatum

Stemless or short-caulescent, 24–35 cm. high. Leaves many in a dense cyathiform rosette, 15 cm. long; sheaths 5 cm. long, dark castaneous; blades ligulate, acuminate, flat, 15 mm. wide, green. Scape erect, slender. Scape-bracts foliaceous, densely imbricate. Inflorescence densely subcapitate, 35 mm. long, 75 mm. in diameter. Primary bracts ovate, acuminate, green, much exceeding the flowers, the lower ones with 2 flowers in each axil. Branches aborted. Floral bracts broadly elliptic, up to 12 mm. long, exceeded by the sepals, membranaceous, densely brown-punctulate. Flowers subsessile. Sepals broadly elliptic, obtuse, 14 mm. long, 11 mm. wide, thin-coriaceous, brown-punctulate.

Costa Rica, Panama.

COCLÉ: north of El Valle de Antón, trail to Las Minas, alt. ca. 1000 m., *Allen 2884*.

PANAMÁ: summit of Cerro Campana, alt. 800–1000 m., *Allen 2215*.

5. *THECOPHYLLUM PEDICELLATUM* Mez & Wercklé in *Bull. Herb. Boiss.* II. 3:136. 1903.

Stemless, 5–9 dm. high. Leaves many, 30–65 cm. long; sheaths large, dark brown toward base, coarsely pale-appressed-lepidote toward apex; blades ligulate, acute or subobtuse, 25–90 mm. wide. Scape stout, about equaling the leaves. Scape-bracts erect, mostly imbricate. Inflorescence cylindric, 25–50 cm. long, glabrous. Primary bracts lance-ovate, exceeded at least by the flowers. Branches from rather short in the Costa Rican specimens to 10 cm. long in the Panamanian, erect, slender, lax. Floral bracts membranaceous, shorter or longer than the pedicels. Flowers spreading, often secund. Pedicels slender, 1–2 cm. long. Sepals broadly obovate, asymmetric, obtuse, 7–11 mm. long, convex, ecarinate, coriaceous, even, free. Petals oblanceolate, obtuse, 15 mm. long. Capsules slenderly ellipsoid, acuminate, 25 mm. long.



Fig. 129
Thecophyllum
pedicellatum

Costa Rica, Panama.

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete District, alt. 1800 m., *Davidson 307*.

The single Panamanian specimen has much larger leaves, branches and floral bracts than are usual, but it is too old to show whether these are supported by other characters which would distinguish it specifically.

6. *THECOPHYLLUM CRASSIFLORUM* Mez & Wercklé in Bull. Herb. Boiss. II. 3:138. 1903.

Plant 1 m. high. Leaves 5–6 dm. long; sheaths elliptic, inconspicuous; blades ligulate, acuminate, 4 cm. wide, green, concolorous. Scape stout, 5 dm. long. Scape-bracts exceeding the internodes, the lower ones erect, narrowly triangular, the upper ones elliptic-ovate with short reflexed blades. Inflorescence densely cylindric but interrupted at base, 2–3 dm. long, 4 cm. thick. Primary bracts suberect with bright red recurved apices, broadly ovate, triangular-acute, inflated, the lower ones exceeding the flowers. Floral bracts strongly asymmetric, obliquely truncate, 12 mm. long, 8 mm. wide, coriaceous, subglabrous. Flowers 1 or 2 in the axil of each primary bract, sessile or subsessile, 30 mm. long. Sepals subelliptic, obtuse, asymmetric, 16 mm. long, 14 mm. wide, thick, coriaceous, even, dull.



Fig. 130
Thecophyllum crassiflorum

Costa Rica, Panama.

CHIRIQUÍ: Potrero Muleto to summit, Volcán de Chiriquí, alt. 3500–4000 m., Woodson & Schery 453.

5. *GUZMANIA* R. & P.

GUZMANIA R. & P. Fl. Peruv. 3:37. 1802.

Caraguata Lindl. in Bot. Reg. 13: under *pl.* 1068. 1827.

Davillea Bertero ex Schultes in R. & S. Syst. Veg. 7:1229. 1830, in synon.

Massangea E. Morr. in Belg. Hort. 27:59, 199. 1877.

Sodihoa André in Bull. Soc. Bot. France 24:167. 1877.

Schlumbergera E. Morr. in Belg. Hort. 33:46. 1883, non *Schlumbergera* Lemaire, 1858.

Chirripoa Suessenguth in Engler's Bot. Jahrb. 72:293, *pl.* 4, *Abb.* 11. 1942.

Plant usually stemless and epiphytic. Leaves entire, the sheaths usually conspicuous. Inflorescence simple or compound, the spikes always polystichous-flowered. Flowers perfect. Sepals usually connate. Petals connate or closely agglutinated, naked, yellow or white. Stamens usually included, the filaments appearing more or less fused to the petals. Ovary wholly superior, glabrous. Ovules numerous. Capsule septicidal. Seeds with a long basal straight usually brownish coma.

a. Inflorescence simple.

b. Inflorescence cyathiform, the outer bracts much enlarged, red..... 1. *G. MINOR*

bb. Inflorescence not cyathiform, the outer bracts relatively inconspicuous.

c. Sepals connate for much less than half their length; floral bracts imbricate, exceeding the sepals.

d. Floral bracts membranaceous.

e. Inflorescence cylindric; sepals coriaceous..... 2. *G. MONOSTACHIA*

ee. Inflorescence fusiform; sepals membranaceous.

f. Leaf-blades not over 10 mm. wide; plant more or less caulescent; inflorescence sterile toward apex..... 3. *G. ANGUSTIFOLIA*

- ff. Leaf-blades 20–25 mm. wide; plant stemless; inflorescence fertile throughout..... 4. *G. NICARAGUENSIS*
 dd. Floral bracts coriaceous, lustrous..... 5. *G. CORIOSTACHYA*
 cc. Sepals connate for more than half their length; floral bracts equaling or shorter than the sepals and enfolding them, not imbricate.
 d. Inflorescence very lax; leaf-blades with fine brown stripes..... 6. *G. DISSITIFLORA*
 dd. Inflorescence densely subglobose; leaf-blades with fine wavy transverse lines..... 7. *G. MUSAICA*
 aa. Inflorescence compound.
 b. Floral bracts equaling or exceeding the sepals; spikes densely strobilate.
 c. Inflorescence short and compact; the spikes pressed together..... 8. *G. GLOMERATA*
 cc. Inflorescence elongate and interrupted..... 9. *G. POLYCEPHALA*
 bb. Floral bracts shorter than the sepals.
 c. Branches dense, not much over 4 cm. long at most.
 d. Inflorescence digitate, subcorymbose..... 10. *G. SUBCORYMBOSA*
 dd. Inflorescence cylindric to pyramidal.
 e. Sepals twisted into a slender tube; primary bracts bright red..... 11. *G. DONNELLSMITHII*
 ee. Sepals forming an ellipsoid; primary bracts and the rest of the inflorescence bright yellow..... 12. *G. ZAHNII*
 cc. Branches lax, 10–12 cm. long; sepals connate for 10 mm..... 13. *G. GUATEMALENSIS*

1. *GUZMANIA MINOR* Mez in DC. Monogr. Phan. 9:901. 1896.

Leaves many, densely rosulate, suberect, 3 dm. long, exceeding the inflorescence; sheaths distinct, ovate, punctate-lepidote; blades ligulate, acute or acuminate with a caudate apex, 25 mm. wide or less, glabrous above, obscurely punctate-lepidote beneath. Scape very short, glabrous. Scape-bracts densely imbricate, elliptic-lanceolate, acuminate, 65 mm. long, the lower green, the upper bright red and forming a showy involucre exceeding the flowers. Inflorescence simple, few-flowered, corymbiform. Floral bracts like the upper scape-bracts but slightly cucullate, smaller and thinner. Flowers 35 mm. long. Pedicels short. Sepals linear-oblong, acute, free. Petals linear, obtuse, white, agglutinated for most of their length. Stamens about equaling the petals, high-connate. Capsule subprismatic, about 3 cm. long.

Nicaragua, Costa Rica, Panama, Brazil.

BOCAS DEL TORO: *von Wedel 213*; hills behind Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel 2208*; Shepherd Island, vicinity of Chiriquí Lagoon, *von Wedel 2738*. COCLÉ: El Valle de Antón and vicinity, alt. 500–700 m., *Seibert 455*; mountain forest, vicinity of El Valle, *Bartlett & Lasser 16677, 16703*. PANAMÁ: Cerro Campana, alt. 1000 m., *Allen 2431*. CANAL ZONE: Matachin, *Kuntze 1938*; Caño Quebrado, *Pittier 6687*; headwaters of the Río Chinilla, above Nuevo Limón, *Maxon 6881*; hills north of Frijoles, *Standley 27458*; Barro Colorado Island, *Standley 31376, 40879, 41039, Kenoyer 213, Bailey 39*; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen 17034*. DARIÉN: Cana-Cuasi Trail (Camp 2), Chepigana District, alt. 600 m., *Terry 1429*.

2. *GUZMANIA MONOSTACHIA* (L.) Rusby ex Mez in DC. Monogr. Phan. 9:905. 1896.

Renalmia monostachia L. Sp. Pl. 287. 1753.

Tillandsia monostachia L. Sp. Pl. ed. 2. 410. 1762.

Tillandsia clavata Lam. Encyc. 1:617. 1785.

Pourretia sympaganthera R. & P. Syst. Veg. Fl. Peruv. 1:82. 1789.

Guzmania tricolor R. & P. Fl. Peruv. 3:38, pl. 261. 1802.

Guzmania comosa Bertero ex Schultes in R. & S. Syst. Veg. 7:1232. 1830.

Guzmania sympagantha (R. & P.) Beer, Bromel. 103. 1857.

Tillandsia pachycarpa Baker in Jour. Bot. 25:238. 1887.

Tillandsia gymnophylla Baker in Jour. Bot. 26:41. 1888.

Guzmania platysepala Mez & C. F. Baker in Bull. Torr. Bot. Club 30:437. 1903.

Guzmania clavata (Lam.) Urb. in Fedde Rep. Spec. Nov. 15:99. 1917.



Fig. 131. *Guzmania monostachia*

Stemless, 2–4 dm. high. Leaves many, soon glabrous; sheaths broadly ovate, brownish; blades ligulate, acute, 2 cm. wide, yellow-green. Scape erect, short. Scape-bracts imbricate, ovate, acute, pale green. Inflorescence simple, cylindric, acute, 8–15 cm. long, 2–3 cm. thick, sterile toward apex. Floral bracts imbricate, ovate, acute, membranous, the fertile ones pale with brown stripes, about equaling the flowers, the sterile bright red. Flowers 23–29 mm. long. Sepals 18 mm. long, obovate, broadly obtuse, coriaceous, equally connate for about one fourth their length. Petals white, high-connate, the lobes elliptic, obtuse. Capsule cylindric, 2–3 cm. long. Coma white.

Southern Florida, West Indies, Nicaragua, Costa Rica, Panama, northwestern South America.

BOCAS DEL TORO: Río Cricamola between Finca St. Louis and Konkintoë, alt. ca. 10–50 m., Woodson, Allen & Seibert 1891; Isla Colón, von Wedel 70; indefinite, von Wedel 214a; Water Valley, vicinity of Chiriquí Lagoon, von Wedel 1706; hills behind Fish Creek, vicinity of Chiriquí Lagoon, von Wedel 2448. CANAL ZONE: Werner 53; Las Cascadas Plantation, near Summit, Standley 20001; Barro Colorado Island, Bailey 105, Shattuck 763, Aviles 927; westerly arm of Quebrada Salamanca, alt. 70 m., Dodge, Steyermark & Allen 17032, 17035; Río Chilibre, tributary of Chagres River between Juan Mina and Madden Dam, Bartlett & Lasser 16422.

3. *GUZMANIA ANGUSTIFOLIA* (Bak.) Wittm. in Engler's Bot. Jahrb. 11:62. 1889.

Caraguata angustifolia Baker in Gard. Chron. II. 22:616. 1884.

Guzmania Bulliana André in Rev. Hort. 58:324. 1886.

Guzmania caulescens Mez & Sodiro in Bull. Herb. Boiss. II. 5:112. 1905.

Stem from quite short to about 2 dm. long. Leaves densely imbricate, 8–30 cm. long, green above, purplish beneath; sheaths distinct, elliptic, densely brown-punctulate; blades linear-triangular, acuminate, 10 mm. wide, suberect or somewhat spreading, punctulate-lepidote. Scape slender, short. Inflorescence simple, few-flowered, thick-fusiform, up to 65 mm. long and 40 mm. thick, sterile toward apex. Floral bracts ample, ovate-elliptic, acute or subacuminate, erect, barely shorter than the petals at anthesis, membranaceous, bright red with dark tips.

Fig. 132. *Guzmania angustifolia*

Flowers subsessile. Sepals elliptic, obtuse, 15–20 mm. long, membranaceous, glabrous, connate for 3 mm. Petals bright yellow, 7 cm. long, connate in a slender tube for 6 cm., the free lobes sub-elliptic, obtuse. Stamens included; filaments connate with the petals for nearly their whole length. Capsule prismatic, acute, 28 mm. long.

Costa Rica, Panama, Colombia, Ecuador.

CHIRIQUÍ: Mount Chiriquí, *Pfau* 230 (Mez!).
DARIÉN: Mount Pirri, alt. 1500 m., *Goldman* 1882;
Cana-Cuasi Trail, Real District, alt. 1650 m., *Terry* 1544, 1579, 1598.

4. *GUZMANIA NICARAGUENSIS* Mez & C. F. Baker
in Bull. Torrey Bot. Club 30:436. 1903.

Guzmania bracteosa sensu Donn. Smith in Bot. Gaz. 47:262. 1909, non André ex Mez.

Leaves 10–15 in a dense cyathiform rosette, 3–6 dm. long, usually much exceeding the inflorescence, densely pale-appressed-lepidote beneath, often red-striped; sheaths ovate, 1 dm. long, castaneous toward base; blades ligulate, acute, apiculate, 20–25 mm. wide. Scape erect. Scape-bracts densely imbricate, the lower foliaceous, the upper broadly elliptic, apiculate, subinflated, bright red to reddish brown. Inflorescence simple, densely fusiform, few-flowered, fertile throughout, 7–10 cm. long, glabrous. Floral bracts like the upper scape-bracts but not apiculate, 5 cm. long, membranaceous. Flowers short-pedicellate. Sepals subelliptic, broadly obtuse, to 25 mm. long, membranaceous, short-connate. Petals connate into a slender tube for most of their length, over 6 cm. long, yellow, the free lobes elliptic, obtuse. Stamens barely included, the filaments highly connate with the petals.

Guatemala, Nicaragua, Costa Rica, Panama.

COCLÉ: north of El Valle de Antón, near La Mesa, alt. ca. 1000 m., *Allen* 2803.

5. *GUZMANIA CORIOSTACHYA* (Griseb.) Mez in DC. Monogr. Phan. 9:914. 1896.

Caraguata coriostachya Griseb. in Nachr. Ges. Wiss. Gött. 1864:21. 1865.

Tillandsia nigrescens André, Enum. Bromel. 8. 13 Dec. 1888; in Rev. Hort. 60:568. 16 Dec. 1888.

Guzmania strobilifera Mez & Wercklé in Bull. Herb. Boiss. II. 5:110. 1905.

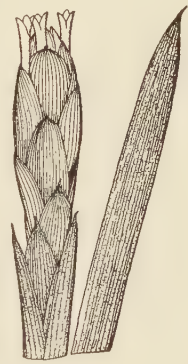
Fig. 133
Guzmania nicaraguensis



Fig. 134
Guzmania
coriostachya

Plant 4–10 dm. high. Leaves rosulate, suberect, 3–6 dm. long; sheaths narrowly ovate, very finely brown-lepidote, castaneous toward base; blades ligulate, acute to acuminate, 15–30 mm. wide, glabrous above, very obscurely lepidote beneath. Scape erect, 5–8 mm. thick. Scape-bracts densely imbricate, the lower subfoliaceous, the upper ovate with triangular apex. Inflorescence simple, strobilate, many-flowered, ovoid or cylindric, 5–8 cm. long, 2–3 cm. thick, glabrous. Floral bracts erect, suborbicular with a broadly triangular obtuse apex, ecarinate, 12–18 mm. long, coriaceous, even, lustrous, bright red, drying pale to castaneous. Flowers subsessile. Sepals ovate, obtuse, 13–16 mm. long. Corolla white, 6–10 mm. longer than the sepals, its lobes elliptic, obtuse.

Costa Rica, Panama, Colombia, Venezuela.

COCLÉ: hills north of El Valle, *Allen* 2945.

6. *GUZMANIA DISSITIFLORA* (André) L. B. Smith in Contrib. Gray Herb. 104:74. 1934.

Sodirola dissitiflora André, Enum. Bromel. 5. 13 Dec. 1888; in Rev. Hortic. 60:565. 16 Dec. 1888.

Usually stoloniferous, 4–9 dm. high. Leaves rosulate, suberect, 3–9 dm. long; sheaths elliptic, dark castaneous at base, the rest pale green with fine brown stripes, densely and finely lepidote; blades linear, acuminate, 7–12 mm. wide, obscurely lepidote beneath. Scape erect, 3–5 mm. thick. Scape-bracts imbricate, the lower foliaceous, the upper elliptic, acute, glabrous, bright red. Inflorescence simple, very lax, 7- to 12-flowered. Axis nearly straight, slender. Floral bracts like the upper scape-bracts, usually shorter than the sepals and closely enfolding them. Flowers spreading. Pedicels slender, 5–8 mm. long. Sepals 3–5 cm. long, thin, glabrous, connate into a slender tube for more than half their length, the free segments oblong, obtuse. Petals white when dry. Capsule slenderly cylindric, equaling the sepals.

Costa Rica, Panama, Colombia.

COCLÉ: vicinity of El Valle de Antón, alt. ca. 600 m., *Allen* 2055; vicinity of La Mesa, north of El Valle de Antón, alt. 1000 m., *Allen* 2383, 2786.

7. *GUZMANIA MUSAICA* (Linden & André) Mez in DC. Monogr. Phan. 9:898. 1896.

Tillandsia musaica Linden & André in Ill. Hortic. 20:171. 1873.

Billbergia musaica (Linden & André) Regel in Gartenfl. 23:378. 1874.



Fig. 135
Guzmania
dissitiflora

Vriesea musaica (Linden & André) Cogn. & March. in Dallière, Pl. Ornem. 2:pl. 39. 1874.

Caraguata musaica (Linden & André) André in Ill. Hortic. 24:27, pl. 268. 1877.

Massangea musaica (Linden & André) E. Morr. in Belg. Hortic. 27:59, 199, pl. 8-9. 1877.

Plant 3-5 dm. high, usually spreading by elongate scaly rhizomes. Leaves 15-20 in a spreading rosette, to 7 dm. long, marked especially beneath with fine



Fig. 136. *Guzmania musaica*

irregular transverse purple-brown lines, obscurely punctulate-lepidote; sheaths short and indistinct, castaneous toward base; blades ligulate, broadly acute or rounded, apiculate, 4-8 cm. wide. Scape erect, somewhat shorter than the leaves. Scape-bracts densely imbricate, broadly elliptic, acute or acuminate, subinflated, bright rose. Inflorescence simple, dense, subglobose, 12- to 25-flowered, glabrous. Floral bracts broadly obovate, apiculate, about half as long as the sepals and enfolding the base of the flower, coriaceous, bright rose. Flowers subsessile. Sepals 25-45 mm. long, oblong,

obtuse, cucullate, highly connate, coriaceous, yellowish. Petals included at anthesis, highly connate. Stamens shorter than the petals.

Panama, Colombia.

COCLÉ: north of El Valle de Antón, near La Mesa, alt. ca. 1000 m., Allen 2781. DARIÉN: rain forest, north slope of divide, Cana-Cuasi Trail, Real (?) District, alt. 1650 m., Terry 1608.

8. *GUZMANIA GLOMERATA* Mez & Wercklé in Fedde Rep. Spec. Nov. 14:256. 1916.



Fig. 137
Guzmania glomerata

Flowering plant nearly 1 m. high, propagating by stout scaly rhizomes. Leaves up to 20 in a dense rosette, erect, coriaceous, 8 dm. long; sheaths broadly elliptic, deep castaneous; blades subglabrous, wholly green, 30 mm. wide. Scape erect, stout. Scape-bracts with castaneous base and short acute erect blade, imbricate. Inflorescence erect, densely capitate from about 10 spikes, 65 mm. thick. Primary bracts broadly ovate, shorter than the spikes, brown. Spikes densely strobiliform, very short-stipitate, suberect, stout, 45 mm. long. Floral bracts elliptic, acute, equaling or slightly exceeding the sepals, submembranaceous. Flowers glabrous. Pedicels 3 mm. long. Sepals lanceolate, acute, 22 mm. long.

Costa Rica, Panama.

COCLÉ: north rim of El Valle de Antón near Cerro Turega, alt. 650-700 m., Woodson & Schery 199. DARIÉN: Cana-Cuasi Trail (Camp 2), Chepigana District, alt. 600 m., Terry 1528.

Plants are identified from the description with which they agree closely except that their sepals appear only slightly connate (10 mm. in the description).

9. *GUZMANIA POLYCEPHALA* Mez & Wercklé in Fedde Rep. Spec. Nov. 14:254. 1916.

Chirripoa solitaria Suessenguth in Engler's Bot. Jahrb. 72:293, pl. 4, Abb. II. 1942.

Over 1 m. high. Leaves 5–10 dm. long; sheaths small, dark castaneous; blades acuminate, to 45 mm. wide, green, subglabrous, rigidly coriaceous. Scape stout. Scape-bracts foliaceous, strict, densely imbricate. Inflorescence many-flowered, cylindric, laxly bipinnate, 3–4 dm. long. Primary bracts broadly ovate, the lower ones suberect, exceeding the spikes and with a long acuminate apex, the upper spreading, equaling or shorter than the spikes and apiculate. Spikes densely strobilate, globose, 20- to 25-flowered, 4–6 cm. long, the lower short-stipitate, the upper sessile. Floral bracts broadly elliptic, emarginate, exceeding the sepals, convex, coriaceous, nerved, glabrous. Pedicels short. Sepals obtuse, 16 mm. long, connate for 2 mm., coriaceous.

Costa Rica, Panama.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., Seibert 208.

10. *GUZMANIA SUBCORYMBOSA* L. B. Smith in Contrib. Gray Herb. 117:10. 1937.

Guzmania compacta sensu L. B. Smith in Contrib. Gray Herb. 98:32. 1932, non Mez.



Fig. 138
Guzmania
subcorymbosa

Plant 3–6 dm. high. Leaves many in a dense cyathiform rosette, usually with fine purple stripes toward base; sheaths ovate, 7 cm. long, densely brown-punctulate, often castaneous toward base; blades linear-triangular, acuminate, 10–15 mm. wide, glabrous above, obscurely punctulate below. Scape erect, slender. Scape-bracts densely imbricate, foliaceous. Inflorescence digitate, subcorymbose, green. Primary bracts ovate, acute, half as long as the axillary spikes, coriaceous, even. Spikes sub-ellipsoid, sessile or subsessile, dense, 3- to 10-flowered, 25–40 mm. long. Floral bracts ovate, broadly acute or obtuse, shorter than the sepals, coriaceous, even, ecarinate, subglabrous. Flowers subsessile. Sepals elliptic, acute, 10–12 mm. long, short-connate, carinate, coriaceous. Petals white. Capsule cylindric, 3 cm.

long.coma red-brown.

Costa Rica, Panama, Colombia.

CANAL ZONE: Gatún. Cultivated material collected by Corbett in 1914.

11. *GUZMANIA DONNELLSMITHII* Mez ex Donn. Smith in Bot. Gaz. 35:9. 1903.

Thecophyllum angustum Mez & Wercklé in Bull. Herb. Boiss. II. 4:1121. 1904.

Plant stemless. Leaves about 15, suberect, 4–6 dm. long, exceeding the in-

florescence; sheaths large, ovate or elliptic, forming a slender pseudobulb, densely brown-lepidote, often finely purple-striped; blades ligulate, acuminate, 2-3 cm. wide, concolorous, pale-lepidote, green. Scape erect, slender. Scape-bracts densely imbricate, foliaceous. Inflorescence densely bipinnate, cylindric, 11-13 cm. long, 4 cm. thick. Primary bracts suberect to spreading, broadly ovate, inflated, bright red, punctulate-lepidote, thin, the lower ones exceeding the flowers and with long acuminate blades. Branches densely 2- to 3-flowered, stipitate, rhachis 10-12 mm. long. Floral bracts suborbicular to reniform, 6-10 mm. long, ecarinate, thin, glabrous, red. Flowers erect. Pedicels very short and stout. Sepals nearly or quite free but twisted into a slender tube, narrow, obtuse, 16-20 mm. long, coriaceous, subglabrous. Petals conglutinated, naked, obtuse, erect, slightly exceeding the sepals. Stamens included.



Fig. 139
Guzmania
Donnellsmitbii

Costa Rica, Panama.

BOCAS DEL TORO: hills behind Fish Creek, vicinity of Chiriquí Lagoon, von Wedel 2333. COCLÉ: north rim of El Valle de Antón, alt. 600-1000 m., Allen 1645; vicinity of La Mesa, north of El Valle de Antón, alt. 1000 m., Allen 2382, 2802.

12. *GUZMANIA ZAHNII* (Hook. f.) Mez in DC. Monogr. Phan. 9:940. 1896.

Caraguata Zahnii Hook. f. in Bot. Mag. 99:pl. 6059. 1873.



Fig. 140. *Guzmania Zahnii*

Stemless or slightly caulescent and branching, about 5 dm. high. Leaves 20 to 30, suberect to spreading, 6 dm. long; sheaths indistinct, obscurely brown-lepidote, flavous with dark red stripes; blades ligulate, acuminate, 27 mm. long, thin, glabrous at maturity, wholly purple-red or green near apex, with red-brown stripes dorsally or on both sides. Scape erect, glabrous, red. Scape-bracts densely imbricate, narrowly lanceolate, acuminate, glabrous, bright scarlet. Inflorescence densely bipinnate, pyramidal or short-thyrsoid, up to 25 cm. long and 10 cm. thick, glabrous, bright yellow throughout. Primary bracts broadly ovate with acuminate lamina, the lower ones purple-tipped and exceeding the spikes. Spikes suberect to spreading, the lower distinctly stipitate, subcapitate, 5- to 12-flowered. Floral bracts broadly elliptic or suborbicular, obtuse, carinate, 10 mm. long. Flowers subsessile. Sepals narrowly elliptic,

obtuse, 18 mm. long, connate for 2.5 mm., carinate. Petals elliptic, obtuse, ca. 3 cm. long, connate for 7 mm. Capsule cylindric, 24 mm. long. Coma subferruginous.

Endemic.

CHIRIQUÍ: Volcán de Chiriquí. Known only from cultivated material, collected by Zahn in 1870.

13. *GUZMANIA GUATEMALENSIS* L. B. Smith in Contrib. Gray Herb. 117:8. 1937.
Guzmania superba Suessenguth in Engler's Bot. Jahrb. 72:299, pl. 4, Abb. 12. 1942.

Probably stemless, 6 dm. high. Leaves over 6 dm. long; sheaths large, ovate, blades ligulate, acute, apiculate, 45 mm. wide. Scape erect, 7 mm. thick. Scape-bracts densely imbricate, foliaceous. Inflorescence laxly bipinnate, subpyramidal, 25 cm. long, glabrous. Primary bracts broadly ovate, acute, reaching only the second flower of the axillary branch. Racemes ascending or spreading, 10–12 cm. long, laxly 10- to 12-flowered, nearly straight. Floral bracts broadly elliptic, obtuse, 2 cm. long, inflated, ecarinate, subcoriaceous, stramineous when dry. Flowers spreading. Pedicels stout, 4 mm. long. Sepals elliptic, obtuse, 25 mm. long, ecarinate, connate for 10 mm. Petals 33 mm. long.



Fig. 141. *Guzmania guatemalensis*

Guatemala, Panama, Colombia.

COCLÉ: vicinity of La Mesa, north of El Valle de Antón, alt. 1000 m., Allen 2368.
DARIÉN: rain forest, Cana-Cuasi Trail near crest, Chepigana District, alt. 1500 m., Terry 1589.

6. CATOPSIS Griseb.

CATOPSIS Griseb. Fl. Brit. W. Ind. 599. 1864.

Tussacia Willd. ex Beer, Bromel. 21, 99. 1857, non Reichenb. 1827.
Pogospermum Brongn. in Ann. Sci. Nat. V. 1:327. 1864.

Stemless herbs. Leaves densely utriculate-rosulate, entire, minutely appressed-lepidote, green, the sheath large. Scape conspicuous. Inflorescence usually bipinnate, rarely simple or tripinnate, exceeding the leaves, its branches polystichous-flowering. Flowers small or minute, usually sessile or nearly so, perfect or functionally dioecious. Sepals free, usually rounded and asymmetric, glabrous. Petals free, naked. Stamens included, unequal so far as known, anthers ovate or elliptic. Ovary superior, broadly ovoid or ellipsoid; style shorter than the ovary or wanting; ovules few to several, long-caudate. Capsule septicidal. Seeds with coma apical and folded over, their bases projecting from the capsule.

- a. Sepals 10–15 mm. long.
 - b. Petals bright yellow, much exceeding the submembranaceous sepals; scape slender, usually decurved..... 1. *C. NUTANS*
 - bb. Petals white, equaling or shorter than the coriaceous sepals; scape erect, stout..... 2. *C. BERTERONIANA*
- aa. Sepals not more than 9 mm. long.
 - b. Scape-bracts shorter than the internodes.
 - c. Sepals not more than 4.5 mm. long; inflorescence delicate with very slender axes; leaves usually 10–15 cm. long..... 3. *C. APICROIDES*
 - cc. Sepals 5–8 mm. long.

- d. Leaves in a cylindric rosette, usually strict; sepals cuneate on the right with the wing much exceeding the midnerve, 5-6 mm. long..... 4. *C. NITIDA*
- dd. Leaves in a cyathiform rosette, arching-divergent; sepals curved on both sides of the base with the wing not exceeding the midnerve, 7-8 mm. long..... 5. *C. SESSILIFLORA*
- bb. Scape-bracts equaling or exceeding the internodes.
- c. Leaf-blades ligulate, 2-4 cm. wide.
- d. Sepals 2 mm. long, exceeding the floral bracts; scape erect..... 6. *C. MICRANTHA*
- dd. Sepals 5-7 mm. long, exceeded by the floral bracts; scape decurved..... 7. *C. WANGERINI*
- cc. Leaf-blades linear, not over 5 mm. wide; flowers barely more than 2-ranked..... 8. *C. LUNDELLIANA*

1. *CATOPSIS NUTANS* (Sw.) Griseb. Fl. Brit. W. Ind. 599. 1864.

Tillandsia nutans Sw. Prodr. 56. 1788.

Tillandsia vitellina Lk., Kl. & Otto, Ic. Pl. Rar. 101. 1843.

Tussacia vitellina (Lk., Kl. & Otto) Kl. ex Beer, Bromel. 99. 1857.

Pogospermum flavum Brongn. in Ann. Sci. Nat. V. 1:328. 1864.

Pogospermum nutans (Sw.) Brongn. l. c. 1864.

Catopsis fulgens Griseb. in Nachr. Ges. Wiss. Gött. 1864:21. 1865.

Catopsis vitellina (Lk., Kl. & Otto) Baker in Jour. Bot. 25:176. 1887.

Plant 14-40 cm. high. Leaves about 10 in a subfasciculate rosette, to 24 cm. long, obscurely punctulate-lepidote, white-cretaeous especially toward base;



Fig. 142. *Catopsis nutans*

sheaths elliptic, about half as long as the blades; blades subtriangular, acuminate, 25 mm. wide. Scape usually decurved, slender. Scape-bracts erect, lanceolate or elliptic, acuminate, typically much shorter than the internodes. Inflorescence simple or rarely few-branched. Primary bracts like the scape-bracts, shorter than the sterile naked base of the spike. Spikes laxly 3- to 15-flowered, to 2 dm. long. Rhachis nearly or quite straight, angled, glabrous. Floral bracts broadly

ovate or elliptic, obtuse or broadly acute, the lower ones barely shorter than the sepals, the upper much shorter. Flowers perfect, erect to spreading. Sepals strongly asymmetric, broadly elliptic, obtuse, 15 mm. long, submembranaceous, nerved, glabrous. Petals ligulate with flaring blade, 2 cm. long, broadly acute or obtuse, bright yellow. Stamens unequal. Ovary ovoid, stout. Style very short but distinct. Capsule ovoid, long-beaked, 15-20 mm. long.

Greater Antilles, Vera Cruz to Panama, Venezuela and Ecuador.

CANAL ZONE: Las Cascadas Plantation, near Summit, Standley 25763, 29671, 29697; near Madden Dam and along Azote Caballo Road near Alahuella, alt. 90-100 m., Dodge 16585.

2. *CATOPSIS BERTERONIANA* (Schultes) Mez in DC. Monogr. Phan. 9:621. 1896.

Renealmia pendula Gaertn. Fruct. 3:13. 1805, non *Catopsis pendula* Bak. 1889.

Tillandsia pendula Thunb. ex Gaertn. l. c.

Tillandsia Berteroniana Schultes in R. & S. Syst. Veg. 7:1221. 1830.

Pogospermum Berteronianum (Schultes) Brongn. in Ann. Sci. Nat. V. 1:328. 1864.

Catopsis Mosenii Mez in DC. Monogr. Phan. 9:622. 1896.

Catopsis nutans sensu L. B. Smith in Ann. Missouri Bot. Gard. 24:180. 1937, non Griseb. 1864.



Fig. 143
Catopsis
Berteroniana

Plant 4–9 dm. high. Leaves several in a subfasciculate rosette, to 4 dm. long, densely white-cretaeous especially toward base, light green; sheaths about as long as the blades, elliptic; blades triangular, acute, 4–5 cm. wide. Scape erect, 5–10 mm. thick, soon glabrous. Scape-bracts erect, the lower foliaceous and densely imbricate, the upper broadly ovate, apiculate, often shorter than the internodes. Inflorescence bipinnate or rarely simple, to 3 dm. long. Primary bracts mostly shorter than the sterile base of the spike, broadly ovate, apiculate. Spikes suberect, long-stipitate, rather laxly many-flowered. Floral bracts broadly ovate to suborbicular, obtuse, 6–8 mm. long, coriaceous. Flowers perfect, suberect. Sepals strongly asymmetric, obovate, to 12 mm. long and 9 mm. wide, equaling or exceeding the petals, coriaceous. Petals ovate-elliptic, white. Stamens unequal. Style distinct, one third as long as ovary. Capsule stoutly ellipsoid, barely exceeding the sepals.

Southern Florida, Greater Antilles, Guatemala, Panama, Trinidad, British Guiana, eastern Brazil.

COCLÉ: western slope and summit of Cerro Valle Chiquito, alt. 700–800 m., Seibert 646; vicinity of El Valle, alt. 100–800 m., Allen 738.

3. *CATOPSIS APICROIDES* (Schlecht. & Cham.) Baker in Jour. Bot. 25:174. 1887.

Tillandsia apicroides Schlecht. & Cham. in Linnaea 6:55. 1831.

Tussacia apicroides (Schlecht. & Cham.) Beer, Bromel. 263. 1857.

?*Catopsis Schindleri* Mez & Wercklé in Bull. Herb. Boiss. II. 4:1124. 1904, as to staminate plant.

?*Catopsis tenuis* Cufodontis in Archivio Bot. 9:181. 1933.



Fig. 144. *Catopsis apicroides*

Plant 12–45 cm. high with the inflorescence extended. Leaves few in a cyathiform rosette, usually 10–15 cm. long, obscurely punctulate-lepidote; sheaths elliptic, often as long as the blades but only slightly wider; blades ligulate, 10–25 mm. wide, the outer often acute, the inner always rounded and apiculate. Scape suberect or decurved, 1–1.5 mm. thick, glabrous. Scape-bracts remote, erect, involute, elliptic, apiculate. Inflorescence laxly bipinnate or rarely the lower branches divided, pyramidal. Axis flexuous to geniculate. Primary bracts like the scape-bracts, barely exceeding the short sterile naked base of the branch. Branches ascending, laxly many-flowered. Rhachis straight, very slender. Floral bracts ovate, 3–4 mm. long, equaling or shorter than the sepals. Flowers dioecious, spreading or subspreading. Sepals asymmetric, broadly elliptic, thin, to 4.5 mm. long. Petals elliptic, obtuse, 6 mm. long. Stamens very unequal in the male flowers. Ovary ovoid. Style short.

Southern Mexico to Panama.

BOCAS DEL TORO: Water Valley, *von Wedel* 1374; Old Bank Island, *von Wedel* 2109; Little Bocas, *von Wedel* 2527; Peach Creek, *von Wedel* 2652; Western River, *von Wedel* 2781. CANAL ZONE: vicinity of Fort Sherman, *Standley* 3111; drowned forest of Quebrada Ancha, *Steyermark & Allen*.

4. *CATOPSIS NITIDA* (Hook.) Griseb. Fl. Brit. W. Ind. 599. 1864.

Tillandsia nitida Hook. Exot. Fl. pl. 218. 1827.

Tussacia nitida (Hook.) Beer, Bromel. 100. 1857.

Pogospermum nitidum (Hook.) Brongn. in Ann. Sci. Nat. V. 1:328. 1864.



Fig. 145. *Catopsis nitida*

Up to 45 cm. high. Leaves few in an elongate cylindrical rosette, to 35 cm. long, narrowly scarious-margined, not cretaceous; sheaths very indistinct, about as long as the blades but scarcely wider; blades ligulate, rounded-apiculate, to 4 cm. wide. Scape erect or somewhat curved, slender. Scape-bracts remote, erect, involute, lance-ovate, obtuse and apiculate. Inflorescence laxly compound with simple or rarely divided branches, equaling or exceeding the leaves, 5–20 cm. long, glabrous. Primary bracts lanceolate, acute, much shorter than the usually naked sterile base of the spike. Spikes divergent, 3–12 cm. long, lax. Floral bracts broadly ovate, acute, shorter than the sepals. Flowers perfect. Sepals strongly asymmetric with the left side broadly elliptic and the right side cuneate at base and at the apex expanded into a large wing overtopping the midnerve, 5–6 mm. long, nerved, subcoriaceous. Petals elliptic, obtuse, barely exerted. Style lacking.

Greater Antilles, Guiana, Guatemala, Honduras, Costa Rica, Panama.

CHIRIQUÍ: forest, Bajo Mono, Boquete District, alt. 1350 m., *Davidson* 535; Boquete, alt. 1140 m., *Davidson* 863.

5. *CATOPSIS SESSILIFLORA* (R. & P.) Mez in DC. Monogr. Phan. 9:625. 1896.

Tillandsia sessiliflora R. & P. Fl. Peruv. 3:42. 1802.

Tussacia sessiliflora (R. & P.) Beer, Bromel. 101. 1857.

Pogospermum sessiliflorum (R. & P.) Brongn. in Ann. Sci. Nat. V. 1:328. 1864.

Catopsis nutans var. *erecta* Wittm. in Engler's Bot. Jahrb. 11:71. 1889.

Catopsis modesta Fritz Müller in Gartenfl. 42:717. 1893.



Fig. 146. *Catopsis sessiliflora*

Plant 1–3 dm. high. Leaves 4–13 in a tubular rosette, 8–20 cm. long, obscurely lepidote; sheaths inconspicuous, about as long as the blades but scarcely wider; blades curving outward, ligulate, rounded and apiculate, 12–25 mm. wide, flat, narrowly scarious-margined. Scape erect, slender, glabrous. Scape-bracts erect, much shorter than the internodes, broadly elliptic, apiculate. Inflorescence simple or compound from a few spikes, lax, to 11 cm. long, glabrous. Primary bracts like the scape-bracts, 7–8 mm. long, much shorter than the naked sterile base of the spikes. Spikes divergent, 2–9 cm. long, laxly flowered. Floral bracts broadly ovate, obtuse, much exceeded by the sepals, thin, nerved. Flowers suberect, perfect. Sepals asymmetric, suborbicular, 7–8 mm. long, subchartaceous, nerved,

wrinkled when dry. Petals lance-ovate, barely exserted, white. Stamens unequal. Ovary ovoid. Style very short. Capsule ovoid, distinctly short-beaked, 12 mm. long.

West Indies and southern Mexico to southern Brazil, Colombia and Peru.

BOCAS DEL TORO: Water Valley, *von Wedel* 643; Peach Creek, vicinity of Chiriquí Lagoon, *von Wedel* 2653; Western River, vicinity of Chiriquí Lagoon, *von Wedel* 2788. CANAL ZONE: vicinity of Fort Sherman, *Standley* 31110; Barro Colorado Island, *Standley* 40855, *Shattuck* 604, *Woodworth & Vestal* 594, *Aviles* 18b; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge*, *Steyermark & Allen* 17031; drowned forest of Quebrada Ancha, alt. 70 m., *Steyermark & Allen*. INDEFINITE: *Cowell* 413.

6. *CATOPSIS MICRANTHA* L. B. Smith in Ann. Missouri Bot. Gard. 30:83. 1943.



Fig. 147. *Catopsis micrantha*

Only the staminate plant known, nearly 1 m. high. Leaves many, erect, to 23 cm. long, more or less cretaceous toward base, the margins not contrasting with the rest of the leaf; sheaths longer than the blades but scarcely distinct; blades broadly ligulate, 4 cm. wide, broadly acute, apiculate, sparsely punctulate-lepidote above and densely beneath. Scape erect, slender. Scape-bracts subfoliaceous, densely imbricate. Inflorescence lax, amply tripinnate. Primary bracts suboblong, broadly acute, much shorter than the branches. Branches divergent, 2 dm. long. Spikes elongate, lax, many-flowered. Floral bracts broadly ovate, shorter than the sepals. Staminate flowers sessile, spreading. Sepals asymmetric, broadly obovate, 2 mm. long. Petals 3.5 mm. long, white. Stamens unequal.

Endemic.

BOCAS DEL TORO: hills behind Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel* 2236.

7. *CATOPSIS WANGERINII* Mez & Wercklé in Bull. Herb. Boiss. II. 4:1126. 1904.
Catopsis pusilla Mez & Wercklé in Fedde Rep. Spec. Nov. 14:248. 1916.

Staminate plants 3–4 dm. high. Leaves several in a cyathiform rosette, not over 18 cm. long; sheaths conspicuous, elliptic-ovate, brown-punctulate-lepidote; blades ligulate, acuminate, 22 mm. wide, glabrous. Scape decurved, very slender, equaling or exceeding the leaves. Scape-bracts lanceolate, acuminate, equaling or exceeding the internodes. Inflorescence compound with simple or compound branches, 15 cm. long, glabrous. Primary bracts like the scape-bracts, slightly exceeding the sterile bases of the axillary branches. Spikes 5 cm. long, dense, or subdense. Floral bracts elliptic, acute, cucullate above the sepals, thin, nerved. Flowers suberect. Sepals asymmetric with the right side produced into a large wing, 5–7 mm. long, chartaceous. Petals narrow, only exserted 2 mm. Stamens unequal.

Pistillate plants 10–25 cm. high. Scape erect or slightly curved, slender, shorter than the leaves. Scape-bracts broadly elliptic, acute, equaling or exceeding the internodes. Inflorescence simple, dense, 3–7 cm. long and 15 mm. thick. Sepals 7 mm. long.

Costa Rica, Panama.

CHIRIQUÍ: Finca Lérída to Peña Blanca, alt. 1750–2000 m., *Woodson & Schery 319*.

8. *CATOPSIS LUNDELLIANA* L. B. Smith in *Contrib. Gray Herb.* 117:6. 1937.



Fig. 148
Catopsis Lundelliana

Plant 25–30 cm. high. Leaves many in a dense subglobose rosette, 1 dm. long, densely and obscurely punctulate-lepidote; sheaths narrowly ovate or elliptic, 15–30 mm. long, not inflated; blades linear, acuminate, 5 mm. wide, involute toward apex. Scape erect, very slender, glabrous. Scape-bracts exceeding the internodes, lanceolate with a long narrow acuminate blade. Inflorescence lax, of 3–4 branches, 7–12 cm. long. Primary bracts like the upper scape-bracts, shorter than the sterile bases of the branches. Spikes divergent, straight, very laxly subtristichous-flowered, to 95 mm. long. Floral bracts broadly ovate, obtuse, thin, prominently nerved, much shorter than the sepals, obscurely lepidote. Flowers suberect. Sepals obovate, obtuse, strongly asymmetric, 5 mm. long, thin, obscurely lepidote. Petals barely exserted, broadly elliptic, obtuse. Stamens unequal. Style short but distinct.

British Honduras, Panama.

CANAL ZONE: Río Medio, *Miller 1754a*.

7. *BROMELIA* L.

BROMELIA L. *Sp. Pl.* 285. 1753.

[*Karatas* Plum. *Gen.* 10. 1703.]

[*Pinguin* Dill. *Hort. Elth.* 320. 1732.]

Karatas Mill. *Gard. Dict. Abr. ed.* 4. 1754.

Pseudomelia Neck. *Elem.* 3:150. 1790.

Agallostachys Beer, *Bromel.* 16, 35. 1857.

Distiacanthus Baker, *Handb. Bromel.* 13. 1889.

Coarse terrestrial herbs, spreading by subterranean stolons. Leaves usually rosulate with large curved spines along the margin. Inflorescence sessile or stipitate, always compound. Sepals free or somewhat united, obtuse or acute, rarely mucronate. Petals rarely with a definite claw, dorsally united by the filaments but their margins free, not appendaged, fleshy in most species. Stamens included,

their filaments forming a long or short tube at base. Anthers narrow, acute. Ovary passing gradually into the thick pedicel, the epigynous tube conspicuous to nearly lacking. Berry succulent, relatively large. Seeds few to many, flattened.

- a. Inflorescence elongate, lax, scapose..... 1. *B. PINGUIN*
 aa. Inflorescence a capitiform panicle sunk in the center of the leaf-rosette, covered with coarse elongate dark brown scales as are also the leaf-bases..... 2. *B. KARATAS*

1. *BROMELIA PINGUIN* L. Sp. Pl. 285. 1753.

Bromelia ignea Beer, Bromel. 35. 1857.

Agallostachys Pinguin (L.) Beer, Bromel. 36. 1857.

Leaves many, rosulate, often over 2 m. long, not constricted between sheath and blade; sheaths very broad, coarsely tomentose-lepidote; blades linear, acumi-



Fig. 149
Bromelia Pinguin

nate, 4 cm. wide, deep green above, pale green and very minutely pale-appressed-lepidote beneath, armed with stout teeth up to 10 mm. long. Scape stout, white-farinose. Scape-bracts foliaceous but with the sheaths roseate and subinflated. Inflorescence many-flowered, narrowly pyramidal, white-farinose. Primary bracts like the scape-bracts but the upper ones entire. Branches to 12-flowered. Floral bracts linear-subulate from a short broad base, 3 cm. long. Flowers to 6 cm. long, distinctly pedicellate. Sepals erect, very narrowly triangular-subulate, pale. Petals linear-elliptic, 3 cm. long, rose with white base and margins, densely white-tomentose at apex. Ovary slenderly ellipsoid,

2 cm. long. Berry ovoid, about 35 mm. long, yellow or ochraceous, strongly verrucose, acidulous, aromatic.

West Indies, Guiana, Mexico, Central America.

PANAMÁ: forests on dry limestone, around Alajuela, Chagres Valley, alt. 30-100 m., *Pittier* 3482; Chepo, alt. ca. 60 m., *Pittier* 4703; Bella Vista, at sea level, *Killip* 12016. CANAL ZONE: Balboa, *Standley* 25498.

According to Standley, this species is known as *Piñuela* in the Canal Zone and is frequent along the Pacific coast.

2. *BROMELIA KARATAS* L. Sp. Pl. 285. 1753.

Bromelia Acanga L. Syst. Nat. ed. 12. 2:232. 1767, in part.

Bromelia acaulis Stokes, Bot. Mat. Med. 2:204. 1812.

Nidularium Karatas (L.) Lem. ex Griseb. Fl. Brit. W. Ind. 591. 1864.

Karatas Plumieri E. Morr. in Belg. Hortic. 22:131. 1872.

Rosette up to 3 m. in diameter. Leaf-sheaths large, covered with long coarse dark brown scales; blades 3-5 cm. wide, acuminate, pungent, minutely lepidote beneath, laxly armed with coarse curved teeth 5-8 mm. long. Inflorescence many-flowered, flat-topped, surrounded by the red inner leaves. Primary bracts foliaceous. Floral bracts narrowly oblanceolate, attaining the middle of the sepals,



Fig. 150
Bromelia Karatas

entire or sparsely serrate, membranaceous, coarsely lepidote. Flowers 6–9 cm. long. Pedicels short, stout. Sepals lanceolate, acute, lepidote, 3 cm. long. Petals narrowly lanceolate, to 4 cm. long, connate for more than 2 cm., glabrous, rose with white base and margins. Ovary lepidote. Berry fusiform, 8 cm. long, 2 cm. thick, acid, edible.

Mexico and the West Indies to Colombia and Brazil.

PANAMÁ: Chepo, alt. ca. 60 m., Pittier 4701.

Planted for fences and known locally as *Piro*, according to Standley.

8. BILLBERGIA Thunb.

BILLBERGIA Thunb. Pl. Bras. Dec. 30. 1821.

Eucallias Raf. Fl. Tellur. 4:25. 1838.

Jonghea Lemaire in Jard. Fleur. 2: under *pl. 181–182*. 1852.

Cremobotrys Beer in Flora 37:348. 1854.

Helicodea Lemaire in Ill. Hort. 11: *pl. 421*. 1864.

Plants stemless. Leaves usually few; sheaths large; blades spinose-serrate, often banded. Scape erect or decurved; scape-bracts red, thin. Inflorescence simple or compound. Flowers large, showy, usually sessile. Sepals free, erect. Petals free, nearly or quite regular, bearing 2 scales near base, claw long, blade narrow. Stamens exserted at anthesis. Pollen-grains with longitudinal folds but no pores. Epigynous tube large. Ovules many.

1. BILLBERGIA MACROLEPIS L. B. Smith in Contrib. Gray Herb. 114:3, *pl. 1, f. 6*. 1936.

Billbergia pallidiflora sensu Mez in DC. Monogr. Phan. 9:303. 1896, in part.

Plant 1 m. or more long when extended. Leaves to 12 dm. long; sheaths elliptic, large; blades linear-triangular, acuminate, 3 cm. wide, sparsely serrate with nearly straight teeth to 3 mm. long, entire toward apex, densely pale-lepidote, gray-green, marked below with large white spots. Scape decurved, 3–4 mm. thick, sparsely white-floccose at first. Scape-bracts imbricate, lanceolate, acuminate, to 24 cm. long, membranaceous, white-floccose. Inflorescence simple, cylindric, to 4 dm. long, lax, many-flowered, densely white-farinose. Floral bracts spreading or reflexed, narrowly oblong or the uppermost ovate, obtuse and apiculate, to 35 mm. long, all but the uppermost equaling or exceeding the ovary, membranaceous, dark brown when dry. Flowers sessile, suberect to spreading. Sepals symmetric, broadly



Fig. 151
Billbergia macrolepis

ovate, broadly acute and apiculate, equal, 10 mm. long, coriaceous, nerved. Petals linear, acute, to 43 mm. long, 4 mm. wide, bronze-green, spirally recurved at anthesis, bearing 2 coarsely crenate scales at base. Ovary subglobose, 15 mm. long, coarsely sulcate with the ridges soon glabrous, epigynous tube 3 mm. long.

Costa Rica, Panama.

PANAMÁ: Río Tecúmen, *Standley 29383*; Río Tapia, *Standley 30665*. CANAL ZONE: Barro Colorado Island, *Shattuck 373*; drowned forest along Río Chagres between junction with Río Pequení and with Río Indio, alt. 66 m., *Steyermark & Allen 16789*.

9. AECHMEA R. & P.

AECHMEA R. & P. Fl. Peruv. Prodr. 47. 1794. *Nomen conservandum*.

Hoiriri Adans. Fam. Pl. 2:67, 584. 1763.

Oechmea J. St.-Hil. Expos. Fam. 1:103. 1805.

Eriostax Raf. Fl. Tellur. 4:25. 1838.

Pothuava Gaud. Bot. Voy. Bonite, pl. 116, 117. 1847.

Macrochordion de Vriese in Jaarb. Nederl. Maatsch. Tuinb. 1853:14. 1853.

Hoplophytum Beer in Flora 37:348. 1854.

Echinostachys Brongn. ex Planch. Hort. Donat. 25. 1854.

Libonia Lemaire in Ill. Hortie. 2:pl. 48. 1855.

Lamprococcus Beer, Bromel. 21, 103. 1857.

Ortgiesia Regel in Gartenfl. 16:193. 1867.

Large or medium-sized stemless herbs. Leaves rosulate. Scape usually conspicuous. Inflorescence of various types. Flowers usually sessile. Sepals usually asymmetric, usually mucronate, free or connate. Petals free, bearing 2 scales each. Second series of stamens more or less joined to the petals. Pollen grains with 2 or 4 pores or sometimes aborted. Ovules caudate or obtuse. Berry usually dry. Seeds small.

- a. Flowers slenderly pedicellate..... 1. AE. MEXICANA
- aa. Flowers sessile.
 - b. Spikes polystichous-flowered.
 - c. Floral bracts or at least the lower ones serrate or serrulate, nearly or quite as long as the flowers.
 - d. Floral bracts firm, densely serrate or serrulate throughout.
 - e. Spikes globose; inflorescence usually compound..... 2. AE. MAGDALENAE
 - ee. Spikes ovoid or conic to cylindric; inflorescence simple.
 - f. Floral bracts sharply reflexed above the middle, equaling or longer than the mature flowers..... 3. AE. VEITCHII
 - ff. Floral bracts merely spreading above the middle, slightly shorter than the mature flowers..... 4. AE. GERMINYANA
 - dd. Floral bracts membranaceous, the lower ones denticulate toward apex and much exceeding the flowers..... 5. AE. ALLENII
 - cc. Floral bracts entire and much exceeded by the sepals or wanting.
 - e. Floral bracts minute or wanting..... 6. AE. NUDICAULIS
 - ee. Floral bracts conspicuous, the lower ones broad..... 7. AE. TONDUZII
 - bb. Spikes distichous-flowered.
 - c. Floral bracts alate-decurrent and forming a pouch about the flowers below..... 8. AE. TILLANDSIODES
 - cc. Floral bracts not at all decurrent.
 - d. Floral bracts with overlapping edges, forming tubular sheaths about the bases of the flowers..... 9. AE. SETIGERA
 - dd. Floral bracts cymbiform or flat, their edges not meeting.

- e. Floral bracts 5 mm. long; inflorescence bipinnate..... 10. *AE. ANGUSTIFOLIA*
 ee. Floral bracts 10-17 mm. long; inflorescence 2- to 3-pinnate.
 f. Floral bracts imbricate and concealing the rhachis, 14-17
 mm. long, faintly nerved near the margins..... 11. *AE. DACTYLINA*
 ff. Floral bracts spreading and exposing the rhachis, 10-13
 mm. long, prominently and uniformly nerved..... 12. *AE. PUBESCENS*

1. *AECHMEA MEXICANA* Baker in Jour. Bot. 17:165. 1879.

Aechmea Bernoulliana Wittm. in Engler's Bot. Jahrb. 14:Beibl. 32:1. 1891.

Plant 7 dm. to over 1 m. high. Leaves many in a utriculate rosette, 6-12 dm. long; sheaths indistinct, ovate, brown, densely lepidote; blades ligulate, acute to rounded and apiculate, 6-12 cm. wide, serrate with straight spines to 2 mm. long,



Fig. 152
Aechmea mexicana

finely pale-lepidote especially beneath. Scape erect, stout, pale-furfuraceous. Scape-bracts to 18 cm. long, much exceeding the internodes, linear-lanceolate, acuminate, entire, membranaceous, stramineous, pale-lepidote, the upper ones deflexed. Inflorescence amply paniculate, subcylindric to slenderly pyramidal, 3-7 dm. long, furfuraceous. Primary bracts linear to subfiliform, much shorter than the branches, membranaceous. Branches spreading, to 17 cm. long. Racemes laxly few-flowered. Floral bracts filiform, much

shorter than the pedicels. Flowers divergent to spreading. Pedicels slender, 4-16 mm. long. Sepals broadly triangular-ovate, asymmetric, mucronate, 6 mm. long, free. Petals ligulate, emarginate, 10-15 mm. long, red or lilac, bearing 2 scales near base. Ovary globose or ellipsoid, 6 mm. long, often enlarging in fruit. Ovules borne at top of cell, caudate.

Mexico (Vera Cruz), Guatemala, Costa Rica, Panama, Ecuador.

COCLÉ: north of El Valle de Antón, alt. ca. 1000 m., *Allen 2881, 2900.*

2. *AECHMEA MAGDALENÆ* (André) André ex Baker, Handb. Bromel. 65. 1889.

Chevalliera Magdalenæ André, Enum. Bromel. 3. 13 Dec. 1888; in Rev. Hortic. 60:563. 16 Dec. 1888.

Bromelia Magdalenæ (André) C. H. Wright in Kew Bull. 1923:267 1923.

Ananas magdalenæ (André) Standl. ex Standl. & Calderon, Lista Prelim. Pl. S. Salvador, 45. 1925.

Plant about 1 m. high. Leaves several in a laxly crateriform rosette, to 2 m. long; sheaths short and inconspicuous denticulate, covered with minute brown scales; blades linear, acuminate, 5-10 cm. wide, glabrous above, finely pale-lepidote beneath between the nerves, laxly armed with dark uncinat spines up to 5 mm. long; sheaths short and inconspicuous, denticulate, covered with minute brown much exceeding the internodes, the upper ones massed below the inflorescence and reflexed. Inflorescence simple or more often compound from a few subequal heads, compact, broadly pyramidal. Heads sessile, globose, 12 cm. thick. Floral bracts decurved from the middle, ovate with a triangular acuminate pungent apex, to 65 mm. long, coriaceous, thick, densely spinose-serrate, cinereous-lepidote be-



Fig. 153. *Aechmea magdalenae*

neath. Flowers sessile, to 5 cm. long, much compressed dorsally. Sepals asymmetric, narrowly triangular, acuminate, pungent, the anterior one to 38 mm. long, the posterior ones to 35 mm., free, lepidote. Petals 4 cm. long, acute, flavous when dry, bearing 2 minute truncate scales well above base. Ovary broadly elliptic, enlarged in fruit. Ovules borne in upper half of cell.

Mexico, Guatemala, Salvador, Costa Rica, Panama, Colombia, Ecuador.

BOCAS DEL TORO: *Carleton* 278; Water Valley, *von Wedel* 711. CHIRIQUÍ: vicinity of San Bartolomé, Peninsula de Burica, alt. 0–50 m., *Woodson & Schery* 884. PANAMÁ: wet forest, Río Tapia, *Standley* 26142; Río Tecúmen, *Standley* 26753. CANAL ZONE: along Caño Quebrado, *Pittier* 6830; hills north of Frijoles, *Standley* 27613; Gamboa, *Standley* 28411; near Fort Randolph, *Standley* 28652; Darién Station, *Standley* 31633; Barro Colorado Island, *Standley* 31263, *Salvoza* 869, *Aviles* 17, *Bailey* 515, *Shattuck* 117, 420.

Called *Pita* or *Piñuela*. The leaves yield a fiber of good quality.

3. *AECHMEA VEITCHII* Baker in Bot.Mag. 103: pl. 6329. 1877.

Chevalliera Veitchii (Bak.) E. Morr. in Belg. Hortic. 28:177, pl. 9. 1878.

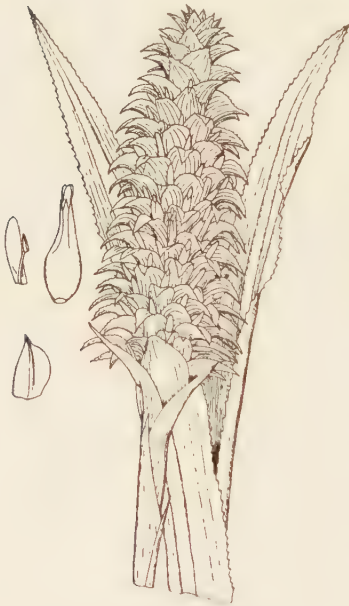


Fig. 154. *Aechmea Veitchii*

Stoloniferous, about 1 m. high. Leaves 12–17 in a loose cyathiform rosette, 3–10 dm. long; sheaths short and indistinct; blades ligulate, abruptly acute, apiculate, pungent, 4–6 cm. wide, glabrous and pale green above with spots of dark green, beneath densely cinereous-lepidote, spinulose with teeth 1 mm. long and 1–2 mm. apart. Scape erect, stout. Scape-bracts densely imbricate, foliaceous, acute or acuminate, spinulose-serrate. Inflorescence simple with flowers many-ranked, dense, cylindric or slenderly conic, 1–4 dm. long, 30–55 mm. thick. Floral bracts equaling or longer than the flowers but with the upper half sharply reflexed, lance-ovate, acuminate, pungent, 12–15 mm. long, densely spinose-serrate, bright red, glabrous above, sparsely white-furfuraceous beneath. Flowers sessile, suberect, 2 cm. long. Sepals free, asymmetric, acute, pungent, 13 mm. long, white with the extreme apex rose. Petals fugacious, ligulate, obtuse, barely ex-

serted, bearing 2 oblique denticulate scales near base. Ovary stoutly obconic, glabrous, white. Ovules pendent from the top of the cell, caudate.

Costa Rica, Panama, Colombia.

DARIÉN: rain forest, north slope of Cana-Cuasi Trail, Real District, alt. 1650 m., *Terry* 1545.

4. *AECHMEA GERMINYANA* (Carr.) Baker, Handb. Brom. 66. 1889.

Chevalliera Germinyana Carr. in Rev. Hort. 53:230. 1881.

Leaves 20–30 in a spreading rosette, often over 1 m. long, subchartaceous; sheaths ovate, distinct, large, densely appressed-lepidote; blades ligulate, subobtuse, ending in a broad brown mucro, closely serrulate with teeth 1 mm. long, appressed-lepidote beneath. Scape stout, erect. Scape-bracts imbricate, lance-elliptic, pungent, serrulate, green. Inflorescence simple, many-flowered, ovoid to cylindric with a small coma of sterile bracts at apex, to 9 cm. long and 65 mm. thick. Floral bracts densely imbricate with apices spreading at anthesis, ovate-elliptic, broadly acute, slightly shorter than the mature flowers, scarlet, appressed-lepidote at first, serrulate, subcoriaceous. Flowers sessile, 32 mm. long. Sepals free, asymmetric, subelliptic, 13 mm. long, mucronulate, glabrous. Petals about twice as long as sepals, acute, white, appendaged about one-fourth up from base. Ovary 6 mm. long, 3-angled, epigynous tube wanting. Berry globose, 7 mm. thick.

Panama, Colombia.

DARIÉN: vicinity of Cana, alt. 1800 m., *Williams* 960.

5. *AECHMEA ALLENII* L. B. Smith in Ann. Missouri Bot. Gard. 28:411, *pl.* 19. 1941.

Stemless, spreading by very stout stolons. Leaves subfasciculate, erect, 6–7 dm. long, much exceeding the inflorescence, densely and minutely appressed-lepidote; sheaths large, narrowly elliptic, entire, scarcely darker than the blades; blades ligulate, broadly acute and mucronate, not at all narrowed at base, to 55 mm. wide, densely serrulate, green. Scape slender, to 35 cm. long, white-flocculose. Scape-bracts densely imbricate, large, oblanceolate, acute, membranaceous, bright rose, denticulate toward apex, flocculose at base. Inflorescence erect, simple, densely ellipsoid, 8–10 cm. long, 4 cm. thick. Floral bracts erect, the lower ones like the scape-bracts and much exceeding the flowers, the upper narrowly lanceolate, acuminate, entire, equaling the sepals or slightly shorter. Flowers sessile. Sepals free, strongly asymmetric, 23 mm. long including the 6 mm. erect mucro, with the ovary densely white-lepidote. Petals 3 cm. long, bearing 2 dentate scales at base, white or pale lilac, ovary orbicular, strongly compressed and 3-angled, to 17 mm. long, epigynous tube crateriform, ovules borne near apex of cell, caudate.

Endemic.

COCLÉ: epiphytic; vicinity of La Mesa, north of El Valle de Antón, alt. 1000 m., *Allen* 2378; trail to Las Minas, north of El Valle de Antón, alt. 1000 m., *Allen* 2467.

6. *AECHMEA NUDICAULIS* (L.) Griseb. Fl. Brit. W. Ind. 593. 1864.

Bromelia nudicaulis L. Sp. Pl. 286. 1753.

Billbergia nudicaulis (L.) Lindl. in Bot. Reg. 13: under *pl.* 1068. 1827.

Billbergia pyramidata Beer, Bromel. 123. 1857.

Hoplophytum nudicaule (L.) K. Koch in Ind. Sem. Hort. Berol. 1856: App. 6. 1857.

Hohenbergia nudicaulis (L.) Baker in Saund. Refug. Bot. under *pl.* 284. 1871.

Potbuava nudicaulis (L.) Regel in Gartenfl. 31:291. 1882.



Fig. 155
Aechmea nudicaulis

Plant very variable in proportions, 3–7 dm. high. Leaves densely fasciculate, 3–10 dm. long; sheaths large, elliptic, forming an urceolate pseudobulb, purple or castaneous, densely brown-lepidote; blades ligulate, broadly obtuse and apiculate, not constricted at base, 6–10 cm. wide, coriaceous, densely pale-lepidote beneath, armed with coarse black teeth to 4 mm. long. Scape slender, erect or decurved, white-floccose. Scape-bracts imbricate, congested below the inflorescence, elliptic, acute, entire, red. Inflorescence a polystichous-flowered cylindric spike, fertile throughout, 5–25 cm. long, pale-floccose at first. Floral bracts small or sometimes wanting, entire. Flowers 22 mm. long. Sepals free, very asymmetric, mucronate, 5–10 mm. long. Petals acute, 12 mm. long, yellow, bearing 2 fimbriate scales. Ovary subglobose, the epigynous tube distinct. Ovules short-caudate, borne at the middle of the cell.

Mexico, Panama, and the West Indies, and a variety in Trinidad and Brazil.

BOCAS DEL TORO: Isla Colón, vicinity of Chiriquí Lagoon, *von Wedel* 37, 115, 1166; Water Valley, *von Wedel* 737.



Fig. 156
Aechmea
Tonduzii

7. *AECHMEA TONDUZII* Mez & Pittier in Bull. Herb. Boiss. II. 3:132. 1903.

Leaves over 1 m. long; the inner sheaths erect, involute, elongate; blades ligulate, broadly obtuse, apiculate, laxly spinulose-serrate, becoming almost entire toward apex, 5 cm. wide, light green, coarsely pale-lepidote beneath. Scape erect, slender, less than a third as long as the leaves. Scape-bracts erect, slightly exceeding the internodes, lanceolate, acuminate into a weak mucro, entire or with a few minute teeth toward apex, membranaceous. Inflorescence a dense spike, cylindric, 7 cm. long, about 16-flowered. Floral bracts spreading to reflexed, triangular, acuminate, sub-pungent, much shorter than the fruiting ovary, entire, the lower ones broad. Sepals free, 3 mm. long including the terminal spine. Berry stout, ovoid, even, 18 mm. long.

Costa Rica, Panama.

DARIÉN: rain forest, Cana Cuasi Trail, near Camp 2, Chepigana District, alt. 1650 m., *Terry* 1529; near crest, alt. 1500 m., *Terry* 1592.

8. *AECHMEA TILLANDSIODES* (Mart.) Baker in Jour. Bot. 17:134. 1879.

Billbergia tillandsioides Mart. ex Schultes in R. & S. Syst. Veg. 7:1269. 1830.

Aechmea vriesioides Baker in Jour. Bot. 17:134. 1879.

Aechmea xiphophylla Baker, Handb. Bromel. 63. 1889.

Leaves fasciculate, very variable in proportions, 5–9 dm. long, minutely appressed-lepidote; sheaths elliptic, 2–15 cm. long, often castaneous toward base; blades linear, acuminate, not narrowed at base, 10–65 mm. wide, densely serrate with straight brown spines to 3 mm. long. Scape much shorter than the leaves, 1–5 mm. thick, sparsely white-flocculose at first. Scape-bracts remote, lanceolate, thin, densely and coarsely serrate, bright red. Inflorescence pinnately compound, fertile throughout, sparsely white-floccose when young. Primary bracts like the scape-bracts, suberect, longer or shorter than the spikes. Spikes suberect, sessile, oblong, 15 mm. wide, dense, distichously 6- to 12-flowered. Rhachis straight, square, stout, wing-angled with the wings adnate to the base of the floral bracts. Floral bracts imbricate at anthesis, then spreading, broadly elliptic, acute, mucronulate, 10–17 mm. long, equaling the sepals, ecarinate, entire, nerved, chartaceous. Sepals asymmetric, elliptic, mucronulate, 7–10 mm. long, subfree. Petals acute, mucronulate, 13–16 mm. long, dark purple with pale margin when dry, bearing 2 fimbriate scales. Ovary much enlarged in fruit. Ovules borne on the upper half of the column, caudate. Berry ellipsoid, 7–10 mm. long.

Represented in Panama only by the following:

AECHMEA TILLANDSIODES var. *KIENASTII* (E. Morr. ex Mez) L. B. Smith in *Caldasia* no. 5:5. 1942.

Aechmea chiriquensis Baker in *Jour. Bot.* 24:243. 1886.

Aechmea squarrosa Baker in *Jour. Bot.* 28:305. 1890, non Baker, 1889.

Aechmea Kienastii E. Morr. ex Mez in *DC. Monogr. Phan.* 9:243. 1896.



Fig. 157. *Aechmea tillandsioides* var. *Kienastii*

Inflorescence digitate or simple or if pinnate then with elongate spikes. Primary bracts spreading or reflexed. Spikes 6- to 30-flowered.

Southern Mexico, Central America, Colombia; the typical variety in Brazil, Guiana and Colombia.

BOCAS DEL TORO: vicinity of Laguna de Chiriquí, *Hart* 173; Water Valley, vicinity of Chiriqui Lagoon, *von Wedel* 1837. COLÓN: around Porto Bello, alt. 5-100 m., *Pittier* 2431. CANAL ZONE: railroad relocation between Gorgona and Gatún, alt. 10-50 m., *Pittier* 2272; Barro Colorado Island, *Shattuck* 830; westerly arm of Quebrada Salamanca, alt. 75 m., *Dodge*, *Steyermark* & *Allen* 17030.

9. *AECHMEA SETIGERA* Mart. ex Schultes in R. & S. Syst. Veg. 7:1273. 1830.

Aechmea Prieuriana Baker, Handb. Brom. 39. 1889.

Plant 1-3 m. high with the inflorescence extended. Leaves 1 m. long, coriaceous; sheaths suborbicular, 9 cm. long, entire, dark brown, covered below with a castaneous membrane, densely subfloccose-lepidote above; blades ligulate, scarcely or not constricted at base, acute or broadly rounded with a broad triangular apiculus, 35-70 mm. wide, glabrous above, densely lepidote beneath, densely spinose-serrate toward base with stout black teeth to 11 mm. long. Scape de-



Fig. 158. *Aechmea setigera*

curved, 13 mm. thick, sparsely tomentose-lepidote. Scape-bracts linear-lanceolate, acuminate, 2 dm. long, coarsely spinose-serrate, subchartaceous, bright red, pale-lepidote. Inflorescence densely bipinnate or the lowest fertile branches divided, cylindric, to 1 m. long and 9 cm. thick, sterile at base and apex and the apices of the remaining spikes or rarely the whole inflorescence. Primary bracts slenderly spiniform from a small triangular base, 3 cm. long, dark brown. Spikes laxly and distichously 2- to 4-flowered. Rhachis 25 mm. long, terete. Floral bracts subreniform, asymmetric, 1 cm. long, forming a tubular sheath about the base of the calyx, green, prominently nerved, bearing a slender dark brown terminal spine to 25 mm. long, those toward the apex of the spike sterile and gradually reduced to just the spine. Flowers sessile. Sepals very asymmetric, subelliptic, obtuse, 16 mm. long, entire, pale yellow-green, free. Petals obtuse, 3 cm. long, pale greenish yellow, bearing 2 fimbriate scales at base. Ovary much enlarged in fruit, the epigynous tube large. Ovules caudate, borne near top of cell.

Panama, Colombia, French Guiana, Amazonian Brazil.

PANAMÁ: Río Tapia, *Standley* 30658. CANAL ZONE: on dead tree in Gatún Lake near Erwin Island, *Shannon*; near Salamanca Hydrographic Station on the gorge of the Río Pequéní, alt. 70-80 m., *Dodge*, *Steyermark* & *Allen* 16076; drowned forest in valley of Río Puente between the Tunnel and Natural Bridge, alt. 70 m., *Dodge* & *Allen* 17323.

10. *AECHMEA ANGUSTIFOLIA* Poepp. & Endl. Nov. Gen. & Sp. 2:43. 1837.

Hoplophytum angustifolium (Poepp. & Endl.) Beer, Bromel. 132. 1857.

Hobenbergia angustifolia (Poepp. & Endl.) Baker in Refug. Bot. 4:pl. 284. 1871.

Aechmea Cumingii Baker in Jour. Bot. 17:227. 1879.

Aechmea boliviana Rusby in Bull. N. Y. Bot. Gard. 4:456. 1907.

Aechmea cylindrica Mez in Fedde Rep. Spec. Nov. 12:413. 1913.

Aechmea inconspicua Harms in Notizbl. 10:786. 1929.



Fig. 159
Aechmea
angustiflora

Plant to 75 cm. high. Leaves 10–15 in an ellipsoid rosette, 5–7 dm. long; sheaths elliptic, 1 dm. long, densely brown-lepidote; blades ligulate, 3–6 cm. wide, cinereous-lepidote, spinose-serrate. Scape erect, white-flocculose, later glabrous. Scape-bracts elliptic, acute, denticulate, red. Inflorescence dense or lax, bipinnate, cylindric, fertile throughout, 15–36 cm. long. Lowest primary bracts like the scape-bracts, exceeding the spikes, the others abruptly reduced to about the size of the floral bracts, ovate or narrowly triangular, acuminate. Spikes spreading or reflexed, distichously 10-flowered, 20–45 mm. long. Rhachis undulate, compressed. Floral bracts spreading, cymbiform, broadly ovate, mucronate, 5 mm. long, barely exceeding the ovary, puberulent. Flowers 12–16 mm. long. Sepals asymmetric, mucronate, free, 4–5 mm. long. Petals linear, mucronate, bearing 2 scales above base. Ovary ellipsoid. Ovules borne at summit of cell, caudate.

Costa Rica, Panama, Colombia, Peru, Bolivia, Brazil.

CANAL ZONE: between Maumé and Gorgona, *Wagner*; drowned forest of upper Río Pequeni between Salamanca Hydrographic Station and Río Boquerón, alt. 70 m., *Allen in hb. Dodge 17272*. DARIÉN: vicinity of Cana, alt. 1800 m., *Williams 845*; Cana-Cuasi Trail, Chepigana District, alt. 1200 m., *Terry 1542*.

11. *AECHMEA DACTYLINA* Baker in Jour. Bot. 17:161. 1879.

Plant over 8 dm. high. Leaves 5–14 dm. long; sheaths very large, elliptic, pale-punctulate-lepidote; blades ligulate, acute, pungent, 45–75 mm. wide, rigid, pale green, serrate with spreading spines up to 1 cm. long. Scape erect, to 1 cm. thick, white-flocculose at first. Scape-bracts erect, imbricate, elliptic, acute or acuminate, entire, pale green or the upper ones red. Inflorescence amply paniculate, subthyrsoid, 25–60 cm. long. Axes angular, white-arachnoid. Primary bracts spreading or reflexed, narrowly lanceolate, acuminate, much shorter than the branches, bright red, sparsely lepidote or glabrous. Branches divergent to spreading, the lower ones usually divided and bearing 2–8 spikes, to 25 cm. long. Spikes linear, acute, 5–16 cm. long, 10–16 mm. wide, complanate, distichous-flowered. Floral bracts densely imbricate, broadly ovate to suborbicular, 14–17 mm. long, equaling or exceeding the sepals, mucronulate with free entire margins, sharply carinate toward apex, coriaceous, glabrous, finely nerved near margin. Flowers sessile, 17 mm. long. Sepals lanceolate, acute, alate, 7–8 mm. long, connate for 1 mm. Petals lingulate, acute, yellow. Stamens included. Ovary angled, gla-



Fig. 160
Aechmea dactylina

brous, the epigynous tube short. Ovules few, borne at top of cell, caudate.

Costa Rica, Panama, Colombia.

BOCAS DEL TORO: Western River, vicinity of Chiriquí Lagoon, *von Wedel* 2787. COLÓN: Chagres, *Fendler* 450. COCLÉ: Bismark, above Penonomé, alt. 600–900 m., *Williams* 630. CANAL ZONE: near Salamanca Hydrographic Station on the gorge of the Río Pequení, alt. 70–80 m., *Dodge, Steyermark & Allen* 16976a; westerly arm of Quebrada Salamanca, alt. 70 m., *Dodge, Steyermark & Allen* 17039.

12. *AECHMEA PUBESCENS* Baker in Jour. Bot. 17:135. 1879.

Plant 4–12 dm. high. Leaves few in a dense utriculate rosette, to 1 m. long, green and chartaceous except for a broad pale subcoriaceous channeled median

portion, the outer leaves bladeless; sheaths broadly elliptic, 15 cm. long, densely brown-punctulate; blades narrowed from base nearly to middle but not truly petiolate, ligulate, acute, apiculate, 25–35 mm. wide, white-appressed-lepidote beneath, soon glabrous above, the basal half laxly serrate with straight or retrorse green teeth to 5 mm. long, the apical half subentire. Scape erect, slender, white-lanate, soon glabrous. Scape-bracts imbricate, lance-ovate, entire, membranaceous, bright red, pale-lepidote. Inflorescence bipinnate or the lower branches divided, oblong or pyramidal, 1–6 dm. long, fertile throughout, lax at least toward base, densely white-floccose at first. Primary bracts narrower than the scape-bracts, the lower ones equaling or exceeding the branches, the upper ones no larger than the floral bracts. Spikes linear, distichously 8- to 16-flowered, dense. Rhachis straight or slightly geniculate, flattened next the flowers. Floral bracts spreading, broadly ovate, acuminate, pungent, 10–13 mm. long, equaling or exceeding

the sepals, entire with free margins, carinate toward apex, nerved. Flowers sessile. Sepals asymmetric, 6 mm. long, mucronulate. Petals obtuse, 10 mm. long, bearing 2 fimbriate scales high above the base. Ovary subellipsoid, 3-angled, slightly enlarged in fruit. Ovules attached near summit of cell.

Honduras, Nicaragua, Costa Rica, Panama, Colombia.

BOCAS DEL TORO: vicinity of Nievécita, alt. 0–50 m., *Woodson, Allen & Seibert* 1855; Isla Colón, *von Wedel* 128; indefinite, alt. ca. 30 m., *von Wedel* 104; Water Valley, *von Wedel* 981; hills behind Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel* 2395, 2442. COLÓN: Chagres, *Fendler* 449. COCLÉ: region north of El Valle de Antón, alt. ca. 1000 m., *Allen* 2905. PANAMÁ: Río Tecúmen, *Standley* 26671; Río Pedro Miguel, near East Paraíso, *Standley* 29092; Juan Díaz, *Standley* 30024; Río Tapia, *Standley* 30682, 30683; between Matías Hernández and Juan Díaz, *Standley* 31030; Sabanas, *Bro. Paul* 332. CANAL ZONE: vicinity of Frijoles, *Piper* 5775; Las Cascadas Plantation, near Summit, *Standley* 25715; Barro Colorado Island, *Kenoyer* 212, *Bailey* 200, *Woodworth & Vestal*



Fig. 161
Aechmea pubescens

630, *Shattuck* 801; drowned forest in valley of Río Puente between the Tunnel and Natural Bridge, alt. 70 m., *Dodge & Allen* 17322. DARIÉN: vicinity of Cana, alt. 600-1950 m., *Williams* 965. INDEFINITE: 1859-60, *Hayes* 893.

A specimen from Bergius in the Linnaean Society was probably collected by Pihl at Portobello, Colón Province.

10. ANANAS Mill.

ANANAS Mill. Gard. Dict. Abr. ed. 4. 1754.

Leaves densely rosulate, scarcely enlarged at base. Scape evident, erect. Inflorescence densely strobiliform, crowned with a tuft of sterile foliaceous bracts. Flowers sessile. Sepals free, obtuse, slightly asymmetric. Petals free, erect, violet or red, each bearing 2 slenderly infundibuliform scales. Stamens included; pollen-grains ellipsoid with 2 pores. Ovaries coalescing with each other and with the bracts and axis to form a fleshy compound fruit, the epigynous tube short. Ovules borne near top of cell.

1. ANANAS COMOSUS (L.) Merrill, *Interpr. Rumph. Amb.* 133. 1917.

Bromelia Ananas L. Sp. Pl. 285. 1753.

Bromelia comosa L. Herb. Amboin. 21. 1754.

Ananassa sativa Lindl. in Bot. Reg. 13: under *pl.* 1068. 1827, *nomen nudum*; Spach, Hist. Vég. 12:400. 1846.

Ananas sativus (Lindl.) Schultes in R. & S. Syst. Veg. 7:1283. 1830.

Ananas Ananas (L.) Voss in Vilm. Blumeng. ed. 3, 1:964. 1895.

Leaves coarsely and laxly spinose-serrate. Scape short, stout. Scape-bracts serrate. Inflorescence large, many-flowered. Floral bracts soon exposing the tops of the ovaries, relatively inconspicuous, weakly serrulate or entire. Syncarp well over 15 cm. long at maturity with copious palatable flesh. Seeds lacking or very rare.

Native of Brazil. Widely cultivated in the tropics and occasionally spontaneous.

Piña, Pine, Pineapple. Cultivated in the Canal Zone and on Taboga Island.

COMMELINACEAE

Succulent annual or perennial herbs. Leaves alternate, the petioles sheathing at the nodes. Inflorescence of simple or compound scorpioid cymes, rarely 1-flowered. Sepals 3, foliaceous, petalaceous, or scarious. Petals 3, equal or very unequal, the third occasionally very greatly reduced, mostly ephemeral and deliquescent. Stamens 1-6, occasionally sterile; filaments frequently bearded with moniliform hairs, equal or strongly unequal; anthers usually with a conspicuous sterile connective. Pistil 2- to 3-celled; capsule loculicidal, containing 3-12 seeds, ordinarily with a striking micropylar pit.

- a. Ultimate branches of the inflorescence composed of individual scorpioid cymes appearing 1-sided superficially, solitary or variously clustered; corolla regular or irregular.
 - b. Cymes variously clustered or compounded, rarely solitary, but not enclosed by a spatheaceous bract.
 - c. Fertile anthers separate; plants caulescent, terrestrial.
 - d. Anthers large, with an inconspicuous connective, dehiscing by apical pores; seeds with a fleshy aril..... 1. *DICHORISANDRA*
 - dd. Anthers small, but with a conspicuous sterile connective, dehiscing longitudinally; seeds dry.
 - e. Inflorescence of solitary cymes or umbellate clusters of cymes; ovary and capsules 3-celled.
 - f. Flowers regular or essentially so, very small..... 2. *ANEILEMA*
 - ff. Flowers very strongly irregular, of moderate size..... 3. *TINANTIA*
 - ee. Inflorescence a dense panicle or thyrses; ovary and capsules 2-celled..... 4. *FLOSCOPA*
 - cc. Fertile anthers fused into a cochleate hood; large acaulescent epiphytes..... 5. *COCHLIOSTEMA*
 - bb. Cymes solitary, enclosed by a conspicuous spatheaceous bract.
 - c. Fruits dehiscent, capsular; sterile stamens with cruciate anthers... 6. *COMMELINA*
 - cc. Fruits indehiscent, pergamentaceous; sterile stamens with sagittate anthers..... 7. *PHAEOSPHAERON*
- aa. Ultimate branches of the inflorescence composed of paired sessile scorpioid cymes appearing as a 2-sided unit superficially, rarely reduced to a solitary flower; corolla regular.
 - b. Cymes subtended only by very inconspicuous scarious or slightly foliaceous bracts.
 - c. Plants small or mediocre; stems creeping below, but erect or ascending above; bracts minute, scarious, not at all leaf-like; stamens 6, usually in 2 dissimilar series..... 8. *TRIPOGANDRA*
 - cc. Small prostrate plants; bracts inconspicuous but slightly foliaceous and obviously similar to the reduced upper stem leaves; stamens 1-6, all essentially similar..... 9. *CALLISIA*
 - bb. Cymes immediately subtended by 2-4 conspicuous foliaceous bracts.
 - c. Stout erect herbs; sepals becoming fleshy in fruit..... 10. *CAMPETIA*
 - cc. Small creeping herbs; sepals withering in fruit.
 - d. Both sepals and petals free..... 11. *TRADESCANTIA*
 - dd. Both sepals and petals fused into narrow tubes..... 12. *ZEBRINA*

Rhoeo discolor (L'Hér.) Hance, a stout succulent herb with sword-shaped leaves purple beneath, is commonly planted in gardens. It is a native of Yucatan.

1. *DICHORISANDRA* Mikan

DICHORISANDRA Mikan, Del. Fl. & Faun. Bras. pl. 3. 1820. *Nomen conservandum*.
Stickmannia Neck. Elem. 3:171. 1791. *Nomen rejiciendum*.
Petaloxis Raf. Fl. Tellur. 2:83. 1836 [1837].

Large or moderate-sized perennial herbs; stem erect or ascending, occasionally weak and clambering. Inflorescence terminal, paniculate, the branches consisting of few- or several-flowered simple scorpioid cymes. Sepals 3, free. Petals 3, free, essentially equal. Stamens 6, rarely 5, all fertile; filaments short, free, naked; anthers ovoid-fusiform, with a narrow inconspicuous connective, dehiscing by apical pores. Ovary 3-celled. Capsule with 3-5 arillate seeds.

1. *DICHORISANDRA HEXANDRA* (Aubl.) Standl. in Standl. & Calderon, *Lista Prelim. Pl. El Salvador*, 48. 1925.

Commelina hexandra Aubl. *Hist. Pl. Guian. Fr.* 1:35. pl. 12. 1775.

Dichorisandra Aubletiana R. & S. *Syst.* 7:1181. 1829.



Fig. 162. *Dichorisandra hexandra*

Plants fairly stout, 1-3 m. tall; stems relatively slender, frequently weak and clambering, glabrous or minutely and irregularly puberulent. Leaves elliptic to obovate-elliptic, acuminate, obtuse at the base, 10-20 cm. long, subsessile, glabrous or indefinitely puberulent beneath; sheaths 1-3 cm. long, glabrous or pubescent, particularly at the orifice. Panicles 3-15 cm. long, bearing rather few to many fairly showy blue, rarely white, flowers 2-3 cm. in diameter; petals tardily deliquescent.

Guatemala to Brazil and Paraguay; in Panama a very frequent herb in lowland forests, ascending to the foothills.

BOCAS DEL TORO: Isla Colón, *von Wedel* 2964; Western River, *von Wedel* 2784; Fish Creek, *von Wedel* 2409; Water Valley, *von Wedel* 1542; Almirante, *Cooper* 224. CANAL ZONE: Río Pequeni, *Woodson, Allen & Seibert* 1593; Cerro Gordo, *Pittier* 3740; Barro Colorado Island, *Standley* 41139. COCLÉ: between Las Margaritas and El Valle, *Woodson, Allen & Seibert* 1235; El Valle de Antón, *Allen* 1978, 1813; Cerro Valle Chiquito, *Seibert* 511. DARIÉN: Río Yape, *Allen* 367. CHIRIQUÍ: San Bartolomé, *Woodson & Schery* 883; Puerto Armuelles, *Woodson & Schery* 824. PANAMÁ: Arraiján, *Woodson, Allen & Seibert* 1395.

This species is quite variable. In Brazil numerous species of *Dichorisandra* have been described, mostly of dubious validity.

2. ANEILEMA R. Br.

ANEILEMA R. Br. *Prodr.* 270. 1810; *Woodson, Ann. Missouri Bot. Gard.* 29:146. 1942.

Murdannia Royle, *Illustr. Bot. Himal.* 403, pl. 95. 1839 [1840].

Tradescantia of many authors, not L.

Small or fairly large, succulent perennials, perhaps annual in some species;

stems erect or decumbent-ascending. Leaves grass-like to fairly large and broad, sheathing at the base. Inflorescence terminal, usually lateral as well, simple or compound, the ultimate branches composed of individual scorpioid cymes subtended by inconspicuous bracts. Flowers small (in our species), regularly 3-merous. Fertile stamens 6, essentially similar, the anthers longitudinally dehiscent, with conspicuous sterile connectives. Ovary 3-celled. Fruit capsular; seeds dry.



Fig. 163
Ancilema geniculatum

1. *ANEILEMA GENICULATUM* (Jacq.) Woodson,
Ann. Missouri Bot. Gard. 29:147. 1942.

Tradescantia geniculata Jacq. Select. Stirp. Am. Bot.
94. pl. 64. 1763.

Mediocre succulent herbs; stems usually creeping below, but erect or ascending above. Leaves ovate or ovate-lanceolate, acuminate, obtuse or rounded at the base, 3-6 cm. long, rather loosely hairy upon both surfaces, sessile or subsessile, the sheaths 0.5-1.0 cm. long, villous. Inflorescence loosely dichotomous, bearing few to many small white flowers. Sepals lance-trigonal, about 0.2 cm. long. Petals white, slightly exceeding the sepals.

Mexico to Brazil and Bolivia; Hispaniola, Puerto Rico, Trinidad, and the Lesser Antilles. Frequent in lowland forests.

BOCAS DEL TORO: Isla Colón, von Wedel 1285; Water Valley, von Wedel 1681; Western River, von Wedel 1750. CANAL ZONE: Barro Colorado Island, Standley 41038; Las Cascadas, Standley 29681; Culebra, Pittier 2222. COCLÉ: Penonomé, Williams 632. DARIÉN: Pinogana, Allen 923.

This species is cultivated in the tropics, as well as in greenhouses in temperate countries, making a pretty subject for hanging baskets.

3. *TINANTIA* Scheidw.

TINANTIA Scheidw. in Otto & Dietr. Allgem. Gartenzeit. 7:364. 1839. *Nomen conservandum*

Pogomesia Raf. Fl. Tellur. 3:67. 1836 [1837].

Mediocre or fairly large, succulent annuals; stems erect or ascending. Leaves rather large, sheathing at the base. Inflorescence terminal, few- or many-flowered, simple or umbellately compounded at the top of a leafless peduncle. Flowers moderately large, pink, violet, or white; sepals 3, conspicuous and somewhat foliaceous; petals 3, very unequal in size and usually in coloring; stamens 6, all fertile,

but the filaments of the 3 upper bearded and those of the lower naked; pistil 3-celled.

- a. Calyx glabrous 1. *T. LEIOCALYX*
 aa. Calyx very densely glandular-pubescent 2. *T. ERECTA*

1. *TINANTIA LEIOCALYX* C. B. Clarke, Bot. Gaz. 18:211. 1893.

Pogomesia leiocalyx (C. B. Clarke) Standl. Fl. Pan. Canal Zone (U. S. Nat. Herb. Contr. 27:) 111. 1928.

Plants 5–25 dm. tall, the stem erect or ascending, usually rooting at the lowermost nodes, pubescent. Leaves ovate to broadly elliptic, acuminate, obtuse or rounded at the base and produced into a narrow winged petiole, 10–20 cm. long, essentially glabrous; sheath 1–3 cm. long, sparingly pubescent. Inflorescence a few- to many-flowered scorpioid cyme, solitary or paired at the tip of a fairly elongate leafless peduncle. Sepals foliaceous, glabrous, about 1 cm. long. Petals somewhat surpassing the sepals, very unequal, the 2 posterior pinkish-mauve, the anterior nearly white; 3 uppermost stamens with copious deep yellowish beards, brownish at base, 3 lowermost naked.

Mexico to Panama, in lowland forest and bush.

BOCAS DEL TORO: Water Valley, *von Wedel* 1481. CANAL ZONE: Río Paraiso, *Standley* 29864. COCLÉ: between Las Margaritas and El Valle, *Woodson, Allen & Seibert* 1286. PANAMÁ: Isla Taboga, *Woodson, Allen & Seibert* 1504.

2. *TINANTIA ERECTA* (Jacq.) Schlecht. *Linnaea* 25:185. 1852.

Tradescantia erecta Jacq. Collect. Bot. 4:113. 1790.

Tradescantia latifolia R. & P. Fl. Peruv. 3:44. pl. 272. 1802.

Tinantia fugax Scheidw. in Otto & Dietr. Allgem. Gartenzeit. 7:365. 1839.

Pogomesia erecta (Jacq.) Standl. Jour. Wash. Acad. Sci. 17:161. 1927.

Mediocre or fairly large succulent annuals; stem erect or ascending, usually rooting at the lowermost nodes, rather inconspicuously pubescent to glabrous. Leaves ovate- to obovate-elliptic, acuminate or obtuse at the tip, gradually narrowed to a broad subpetiolar base, 8–20 cm. long, scatteringly pubescent, particularly beneath; sheath 1.0–1.5 cm. long, scatteringly puberulent. Inflorescence densely glandular-puberulent, bearing few to many rather showy pale pink flowers in scorpioid cymes, either simple or several umbellately compounded at the tip of a more or less elongate, leafless peduncle.

Mexico to Venezuela; Jamaica and Hispaniola; also introduced in tropical Asia. Rather infrequent in highland forests.

CHIRIQUÍ: Volcán de Chiriquí, *Woodson & Schery* 476; *Woodson & Schery* 250; Upper Río Chiriquí Viejo valley, *P. White* 63.

4. FLOSCOPA Lour.

FLOSCOPA Lour. Fl. Cochinch. 192. 1790.

Dithyrocarpus Kunth, Enum. 4:77. 1843.

Mediocre succulent annuals with erect or ascending stems frequently rooting at the lower nodes. Leaves alternate, with basal sheaths. Inflorescence terminal,

diffusely paniculate, bearing very many small deliquescent flowers. Sepals 3, somewhat unequal. Petals 3, very unequal, the anterior much reduced. Stamens 6, rarely 5, in 2 dissimilar series; filaments naked. Pistil 2-celled.

1. *FLOSCOPA ROBUSTA* (Seub.) C. B. Clarke in DC. Monogr. 3:271. 1891.

Dithyrocarpus robustus Seub. in Mart. Fl. Bras. 3¹:255. 1855.

Floscopa Clarkeana O. Ktze. Rev. Gen. 2:720. 1891.

Mediocre annuals 1–2 dm. tall, more or less densely puberulent to glabrate throughout. Leaves elliptic- or oblong-oblancoelate, acuminate, gradually narrowed to a subpetiolar base, 10–30 cm. long; sheaths 1.0–1.5 cm. long, villous. Inflorescence diffusely and densely paniculate, bearing very many small, purple or white flowers, very densely glandular-puberulent throughout. Capsules pergammentaceous, very abundantly produced.

Nicaragua to northern Brazil and Peru; in lowland forest and bush.

BOCAS DEL TORO: Sibubi, Carleton 230; Water Valley, von Wedel 1724; Fish Creek, von Wedel 2328.

5. COCHLIOSTEMA Lem.

COCHLIOSTEMA Lem. Illustr. Hort. 6: Misc. 70. pl. 217. 1859.

Massive succulent acaulescent epiphytes. Leaves rosulate, sheathed at the base. Inflorescences ternate at the several nodes of a large-bracted scape, bearing numerous extremely handsome purple flowers. Sepals 3, somewhat unequal. Petals 3, the posterior equilateral, the 2 anterior falcate, all fringed with moniliform hairs similar to those of the staminal filaments. Fertile stamens 3, united into a cochleate hood enclosing the anthers; staminodia 2. Pistil 3-celled.

1. *COCHLIOSTEMA ODORATISSIMUM* Lem. Illustr. Hort. 6: Misc. 70. pl. 217.

1859; Woodson & Schery, Ann. Missouri Bot. Gard. 29:149. 1942.

Cochliostema odoratum C. Koch & Bouché, Wochenschr. Ver. Gartenb. 340. 1859.

Cochliostema Jacobianum K. Koch & Linden, Wochenschr. Ver. Gartenb. 322. 1867.

Giant acaulescent epiphytes. Leaves rosulate, oblanceolate, acuminate, attenuated at the base into a long subpetiolar base, 4–10 dm. long; the basal sheath about



Fig. 164. *Cochliostema odoratissimum*

1 dm. long, glabrous throughout. Flowering scape rather stout, 3–8 dm. long, erect or pendulous, bearing 3-nate scorpioid cymes at the nodes, each subtended by a showy petalaceous, lanceolate bract 2–6 cm. long. Sepals about 3 cm. long. Petals about equalling the sepals, purple, densely fringed.

Costa Rica (?), Panama, Ecuador, Bolivia; epiphytic in lowland forests in Panama.

BOCAS DEL TORO: Lobo Creek, Chiriquí Lagoon, *von Wedel* 2627; Fish Creek, *von Wedel* 2296.

This is without doubt the most distinctive genus of *Commelinaceae* in its gigantic size, peculiar habit, and complexity of floral structure.

6. COMMELINA L.

COMMELINA L. Sp. Pl. 60. 1753.

Ananthopus Raf. Fl. Ludovic. 20. 1817.

Commelyna Kunth, Enum. 4:35. 1843.

Sauvallea Wright in Sauv. Fl. Cuba, 156. 1873.

Commelinantia Tharp, Bull. Torrey Bot. Club 49:269. 1922.

Small or mediocre, caulescent, subsucculent annuals. Leaves alternate, sheathing at the base. Inflorescences chiefly terminal, simply scorpioid, few-flowered, more or less enclosed by a conduplicate spathaceous bract. Sepals 3, subequal. Petals 3, two posterior equal, the anterior more or less reduced, frequently greatly so. Stamens 6, the upper 3 sterile, with cruciate anthers, the lower 3 fertile. Pistil 2- to 3-celled. Capsules loculicidally dehiscent.

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| a. Flowering spathes rounded and open at the base; plants creeping, relatively small..... | 1. C. DIFFUSA |
| aa. Flowering spathes closed and truncate at the base; plants essentially erect, relatively large..... | 2. C. ELEGANS |

1. COMMELINA DIFFUSA Burm. f. Fl. Ind. 18. *pl.* 7, *fig.* 2. 1768.

Commelina longicaulis Jacq. Collect. Bot. 3:234. 1789.

Commelina pacifica Vahl, Enum. Pl. 2:168. 1806.

Commelina caespitosa Roxb. Fl. Ind. 1:178. 1820.

Commelina ochreatea Schauer, Nova Acta Acad. Leop.-Carol. Nat. Cur. 19: Suppl. 1. 447. 1843.

Weak, creeping, subsucculent annuals, glabrous throughout. Leaves ovate- or oblong-elliptic, obtuse or acute, sessile or subsessile, 1–3 cm. long; sheaths 0.5–1.0 cm. long. Inflorescence terminal, the spathe foliaceous, conduplicate, ovate-cordate, open and rounded at the base. Flowers few, pale blue; sepals 0.2–0.25 cm. long; 2 posterior petals narrowly clawed, 0.3–0.5 cm. long, the anterior rudimentary or obsolete.

Nearly cosmopolitan; very common in waste places in Panama, at widely varying altitudes.

BOCAS DEL TORO: Water Valley, *von Wedel* 990; Nievécita, *Woodson, Allen & Seibert* 1846. CANAL ZONE: between Gatún and Lion Hill, *Pittier* 2560. COCLÉ: Penonomé, *Williams* 346. CHIRIQUÍ: Río Chiriquí Viejo valley, *Seibert* 238; Boquete, *Davidson* 670; Puerto Armuelles, *Woodson & Schery* 831. DARIÉN: Río Yape, *Allen* 363.

2. *COMMELINA ELEGANS* HBK. Nov. Gen. & Sp. 1:259. 1816.*Commelina caripensis* HBK. loc. cit. 260. 1816.*Commelina sulcata* Willd. ex R. & S. Syst. 1:342. 1817.*Commelina babiensis* Willd. ex R. & S. loc. cit. 1817.*Commelina Martiana* Seub. in Mart. Fl. Bras. 3¹: pl. 37, fig. 1. 1855.*Commelina virginica* of many authors, not L.

Plants mediocre or relatively stout, erect or ascending, the stem branching rather frequently, 1.5–6.0 dm. tall, glabrous or essentially so. Leaves elliptic- or oblong-lanceolate, acuminate, obtuse at the base, sessile or subsessile, 3–12 cm. long, glabrous to sparsely pilose upon either surface; sheath about 1–2 cm. long, densely puberulent to glabrate. Inflorescences terminal or subterminal, solitary or paired; spathes conduplicate, foliaceous, broadly ovate, truncate and closed at the base, 1.5–2.0 cm. long, scatteringly pilosulose to glabrate. Sepals 0.3–0.4 cm. long, hyaline. Petals blue, obovate spatulate, the 2 posterior about 1 cm. long, the anterior somewhat reduced.

Tropical and subtropical America from Florida and Texas to Argentina; frequent in waste ground.

CANAL ZONE: Madden Dam, *Seibert* 547; Ancón Hill, *Seibert* 106; Rio Pequeni, *Woodson, Allen & Seibert* 1625; Barro Colorado Island, *Starry* 116; Balboa Heights, *Killip* 3063. COCLÉ: between Aguadulce and Antón, *Woodson, Allen & Seibert* 1218; Penonomé, *Williams* 594. PANAMÁ: Isla Taboga, *Woodson, Allen & Seibert* 1430; between Capira and Potrero, *Dodge & Hunter* s. n.; Bella Vista, *Standley* 25396; Rio Tataré, *Woodson & Schery* 1003; Savana de Alhajuella, *Pittier* 3479.

Known in some districts of Panama as *Codillo*.

7. *PHAEOSPHAERION* Hassk.

PHAEOSPHAERION Hassk. Flora 49:212. 1866; *Woodson, Ann. Missouri Bot. Gard.* 29:150. 1942.

Athyrocarpus Schlecht. Linnaea 26:454. 1855.

Subsucculent annuals. Leaves alternate, sheathing at the base. Inflorescence simply scorpioid, few-flowered, enclosed by a conduplicate, foliaceous, sheathing bract. Sepals 3, free, hyaline, essentially equal. Petals 3, the 2 posterior enlarged, the anterior reduced. Stamens 6, in two series, the upper 3 sterile, with sagittate anthers, the lower 3 fertile. Pistil 3-celled. Fruit indehiscent, pergamentaceous. Closely similar to *Commelina* except in the indehiscent fruit.

- | | |
|---|--------------------------|
| a. Spathes long-pedunculate, solitary, their margins free; fruit dark purple..... | 1. PH. LEOICARPUM |
| aa. Spathes nearly sessile, clustered, their margins united below; fruit whitish..... | 2. PH. PERSICARIAEFOLIUM |

1. *PHAEOSPHAERION LEOICARPUM* (Benth.) Hassk. Flora 49:212. 1866.

Commelina ? *leiocarpa* Benth. Bot. Voy. Sulph. 176. 1844.

Commelina pallida Schlecht. Linnaea 26:454. 1855.

Athyrocarpus leiocarpus (Benth.) Benth. & Hook. ex Hemsl. Biol. Cent.-Am. Bot. 3:386. 1884.

Medium-sized diffuse herbs; stems repeatedly and subdichotomously branching,

relatively slender, minutely scabrous to glabrate. Leaves oblong-elliptic, acuminate, obtuse at the base, 4–12 cm. long, subglaucous, glabrous or somewhat pubescent beneath. Inflorescences both lateral and subterminal, pedunculate; peduncles slender, deflexed, 1.5–3.0 cm. long, minutely scabrid; spathes conduplicate, broadly ovate-cordate, rounded and open at the base, acuminate, 3–5 cm. long, foliaceous, glabrous. Posterior petals long-unguiculate, about 1 cm. long, the anterior ovate, sessile, about 0.5–0.7 cm. long. Capsules ovoid, 0.7–0.9 cm. long, lustrous, deep purple.

Mexico to Venezuela; lowland forests and waste ground.

CANAL ZONE: Corozal, *Standley 27343*; Margarita Swamp, *Maxon & Valentine 7064*; between Ft. Clayton and Corozal, *Standley 29018*.

2. *PHAEOSPHERION PERSICARIAEFOLIUM* (DC.) C. B. Clarke in DC. Monogr. 3:137. 1881.

Commelina persicariaefolia DC. in Redouté, Lil. 8: pl. 472. 1816.

Commelina rufipes Seub. in Mart. Fl. Bras. 3¹:265. 1855.

Phaeosphaerion persicariaefolium (DC.) C. B. Clarke γ. *rufipes* (Seub.) C. B. Clarke, loc. cit. 1881.

Athyrocarpus persicariaefolius (DC.) Hemsl. Biol. Cent.-Am. Bot. 3:386. 1884.

Athyrocarpus rufipes (Seub.) Standl. in Standl. & Calderon, Lista Prelim. Fl. El Salvador, 47. 1925.

Mediocre, erect or ascending herbs 3–6 dm. tall; stem relatively slender, branching infrequently, glabrous or scatteringly pubescent. Leaves elliptic-lanceolate, narrowly acuminate, inequilaterally rounded at the base, 6–12 cm. long, generally ferruginous-pilose to glabrate, subsessile; sheaths 1–2 cm. long, ferruginously pilose, particularly above. Inflorescences subterminal, paired or in clusters of 3's and 4's, sessile or subsessile; spathes broadly ovate, truncate and closed at the base, obtuse or shortly acuminate at the tip, 2–3 cm. long, ferruginous-pilose. Capsules broadly ovoid, about 0.5 cm. thick, pearly white.

Guatemala to Peru; Cuba, Hispaniola, Puerto Rico, Trinidad; lowland forests and bush, also waste ground.

BOCAS DEL TORO: Changuinola valley, *Dunlap 430*. CANAL ZONE: Chagres, *Fendler 454*; Ft. Randolph, *Standley 28640*; Frijoles, *Standley 27481*; Ancón Hill, *Standley 25175*. COCLÉ: Penonomé, *Williams 523*. PANAMÁ: Río Tecúmen, *Hunter & Allen 244*.

8. *TRIOGANDRA* Raf.

TRIOGANDRA Raf. Fl. Tellur. 2:16. 1836 [1837]; emend. Woodson, Ann. Missouri Bot. Gard. 29:150. 1942.

Heminema Raf. loc. cit. 17. 1837.

Descantaria Schlecht. Linnaea 26:140. 1853, nom. subnud.

Disgrega Hassk. Flora 49:215. 1866.

Leptorhoeo C. B. Clarke in Hemsl. Diagn. Pl. Nov. 55. 1880.

Donnellia C. B. Clarke, Bot. Gaz. 33:261. 1902.

Cuthbertia Small, Fl. Southeast. U. S. 237. 1903.

Neodonnellia Rose, Proc. Biol. Soc. Wash. 19:96. 1906.

Tradescantia of many authors, not L.

Subsucculent herbs of small or moderate size; stems creeping below, but erect or ascending above. Leaves alternate, sheathed at the base. Inflorescence terminal or subterminal, solitary or clustered, long-pedunculate, consisting of 2 equal, greatly condensed scorpioid cymes bearing few or several rather small flowers, not subtended by paired leaf-like bracts. Sepals 3, essentially equal. Petals 3, essentially equal. Stamens 6, usually in 2 very dissimilar series, the outer occasionally sterile; in a few species all fertile and essentially similar. Pistil 3-celled.

- a. Stamens essentially similar, all fertile; petals blue; plants small, 1.0–1.5 dm. tall..... 1. *T. FLORIBUNDA*
- aa. Stamens 2 in very dissimilar series; petals pink or white; plants mediocre, 3–8 dm. tall.....
- b. Inflorescence umbelliform, with relatively long pedicels and relatively short peduncles; sepals usually scatteringly glandular-pilose..... 2. *T. CUMANENSIS*
- bb. Inflorescence capituliform, with relatively short pedicels and relatively long peduncles; sepals glabrous..... 3. *T. ELONGATA*

1. *TRIOGANDRA FLORIBUNDA* (Hook. & Arn.) Woodson, Ann. Missouri Bot. Gard. 29:152. 1942.



Fig. 165

Triogandra floribunda

Aneilema floribundum Hook. & Arn. Bot. Beechey Voy. 311. 1840.

Tradescantia filiformis Mart. & Gal. Bull. Acad. Brux. 9²:376. 1842.

Leptorhoeo filiformis (Mart. & Gal.) C. B. Clarke in Hemsl. Diagn. Pl. Nov. 55. 1880.

Leptorhoeo floribunda (Hook. & Arn.) Baill. Hist. Pl. 13:218. 1894.

Small herbs 1.0–1.5 dm. tall; stems slender, branching below, glabrous or minutely pilosulose. Leaves oblong-lanceolate, 1.0–3.5 cm. long, acute to acuminate, glabrous or the margins minutely ciliolate; sheaths 0.3–0.5 cm. long, ciliolate. Inflorescences terminal, infrequently in the upper leaf axils, rather shortly pedunculate, bearing few to several small blue, pedicellate flowers; pedicels 0.4–0.6 cm. long, minutely pilosulose; sepals 0.1–0.15 cm. long; petals 0.2–0.25 cm. long; stamens essentially similar, the filaments naked.

Mexico to Brazil; in meadows, frequently forming dense turfs.

PANAMÁ: Isla Taboga, Woodson, Allen & Seibert 1507; Las Sabanas, Paul 566; Matias Hernández, Pittier 6778; Chepo, Pittier 4512. CANAL ZONE: Gatún, Standley 27301; Summit, Standley 26915; Balboa, Standley 25465.

2. *TRIOGANDRA CUMANENSIS* (Kunth) Woodson, Ann. Missouri Bot. Gard. 29:152. 1942.

Tradescantia cumanensis Kunth, Enum. 4:96. 1843.

Descantaria cumanensis (Kunth) Schlecht. ex Brückn. Notizblatt 10:56. 1927.

Mediocre herbs 3–8 dm. tall; stem creeping below, erect or ascending above, branching infrequently, glabrous or essentially so. Leaves oblong-lanceolate, acuminate, obtuse at the base, 5–12 cm. long, the margins usually ciliolate, other-

wise glabrous; sheaths 1–2 cm. long, somewhat inflated, scatteringly pilose to glabrate. Inflorescences corymbosely clustered in the axils of the upper leaves; peduncles 1–3 cm. long, minutely eglandular-pilosulose. Flowers pink or white; pedicels 0.3–0.5 cm. long, minutely glandular-pilosulose; sepals about 0.2 cm. long, minutely glandular-pilosulose, rarely glabrate.

Mexico to Brazil; in wet meadows in open forests chiefly at higher elevations.

BOCAS DEL TORO: Water Valley, *von Wedel* 1634; Isla Bastimentos, *von Wedel* 2896; Old Bank Island, *von Wedel* 2061; Almirante, *Cooper* 78; Changuinola valley, *Dunlap* 304. CANAL ZONE: Río Boquerón, *Steyermark & Allen* 17248; Barro Colorado Island, *Kenoyer* 222; Ft. San Lorenzo, *Maxon & Valentine* 7018; Gatún, *Hayes* 240; Chagres, *Fendler* 452. COCLÉ: Penonomé, *Williams* 426. CHIRIQUÍ: Finca Lérica to Boquete, *Woodson, Allen & Seibert* 1144. DARIÉN: Boca de Cupe, *Allen* 890. PANAMÁ: Río Trinidad, *Seibert* 638; Matías Hernández, *Standley* 28930.

It is quite possible that this species is merely a variety of *T. multiflora* (Sw.) Woodson, as may also be the case with the following:

3. *TRIOGANDRA ELONGATA* (G. F. W. Meyer) Woodson, Ann. Missouri Bot. Gard. 29:152. 1942.

Tradescantia elongata G. F. W. Meyer, Fl. Esseq. 146. 1818.

Descantaria elongata (G. F. W. Meyer) Brückn. Notizblatt 10:56. 1927.

Mediocre herbs 3–7 dm. tall; stems relatively slender, creeping below, erect or ascending above, branching infrequently, glabrous. Leaves oblong-lanceolate, acuminate, obtuse at the base, sessile or subsessile, 4–10 cm. long, the margin ciliolate, otherwise glabrous; sheaths 0.5–1.0 cm. long, scatteringly pilose. Inflorescences terminal and axillary at the upper leaf nodes, conspicuously pedunculate; peduncles 1–3 cm. long, slender, eglandular-pilosulose. Flowers pink or white; pedicels 0.1 cm. long or less, glabrous; sepals ovate, 0.15 cm. long, glabrous; petals 0.2–0.25 cm. long.

Guatemala to Paraguay and Brazil; in meadows and open woods, chiefly at lower altitudes.

BOCAS DEL TORO: Water Valley, *Wedel* 1527. CANAL ZONE: Miraflores Lake, *Hunter & Allen* 774; Barro Colorado Island, *Standley* 41079; Gatún, *Hayes* 40. PANAMÁ: Río Tataré, *Woodson & Schery* 1001.

Doubtfully distinct from *T. cumanensis*.

9. CALLISIA L.

CALLISIA L. in Loeffl. It. Hisp. 305. 1758.

Hapalanthus Jacq. Select. Stirp. Am. Bot. 11. pl. II. 1763.

Spironema Lindl. Bot. Reg. pl. 47, Miscel. 26. 1840.

Tradescantella Small, Fl. Southeast. U. S. 238. 1903.

Small prostrate succulent herbs (in Panama); stem branching repeatedly, rooting at the nodes. Leaves sheathing at the base. Inflorescences terminal, also occasionally in the upper nodes, umbelliform, few-flowered, subtended by 2 small foliaceous bracts similar to the upper reduced leaves. Sepals 3, equal, scarious or

very slightly foliaceous. Petals 3, essentially equal. Stamens 6 (in Panama), all fertile and essentially similar. Pistil 3-celled.

1. *CALLISIA CORDIFOLIA* (Sw.) Anders. & Woods. Contr. Arn. Arb. 9:117. 1935.

Tradescantia cordifolia Sw. Prodr. Veg. Ind. Occ. 57. 1783.

Leiandra cordifolia (Sw.) Raf. Fl. Tellur. 2:16. 1836[1837].

Callisia meiandra Sauvalle, Fl. Cub. 159. 1873.

Tradescantia Floridana S. Wats. Proc. Amer. Acad. 17:381. 1882.

Tradescantella Floridana (S. Wats.) Small, Fl. Southeast. U. S. 238. 1913.

Small creeping herbs; stems slender, rooting at the nodes, glabrous. Leaves ovate to ovate-lanceolate, acuminate, rounded at the base, sessile, 0.5–3.0 cm. long, greatly reduced toward the inflorescence, glabrous; sheaths 0.2–0.5 cm. long, glabrous. Inflorescence umbelliform, few-flowered, terminal, occasionally also lateral in the axils of the reduced upper leaves, subtended by 2 inconspicuous, slightly foliaceous bracts 0.1–0.3 cm. long; pedicels 0.2–0.3 cm. long, minutely puberulent. Flowers inconspicuous, white; sepals lanceolate, 0.15–0.2 cm. long, scarious or very slightly foliaceous; petals about 0.25 cm. long.

Peninsular Florida and southeastern Mexico to northern Colombia; Greater Antilles. In wet forests and fields at low elevations.

CANAL ZONE: Darién Station, Standley 31545; Las Cascadas, Pittier 2593. COCLÉ: Bismarck, Williams 614. PANAMÁ: Old Panamá, Killip 3231; Río Tecúmen, Standley 26742.

10. *CAMPELIA* L. C. Rich.

CAMPELIA L. C. Rich. Anal. Fruit. 46. 1808.

Zanonia Cram. Diss. Syst. 75. 1803, non L.

Sarcoperis Raf. Fl. Tellur. 2:16. 1836 [1837].

Gonatandra Schlecht. Linnaea 24:659. 1851.

Massive subsucculent herbs. Leaves alternate, sheathing at the base. Inflorescences terminal on very slender, frequently compound, lateral peduncles, umbelliform, several-flowered, subtended by 2–4 conspicuous foliaceous bracts. Sepals 3, becoming fleshy in fruit, free, essentially equal. Petals 3, essentially equal, free. Stamens 6, the filaments of the outer slightly shortened. Pistil 3-celled. Fruit capsular, enclosed by the fleshy sepals.

1. *CAMPELIA ZANONIA* (L.) HBK. Nov. Gen. & Sp. 1:264. 1816.

Commelina Zanonia L. Sp. Pl. 61. 1753.

Tradescantia Zanonia (L.) Sw. Fl. Ind. Occ. 1:604. 1797.

Zanonia bibracteata Cram. Diss. Syst. 75. 1803.

Commelina bibracteata (Cram.) Wied-Neuwied, Beitr. Bras. 15. 1823.

Tradescantia capitata Vell. Fl. Flum. 3: pl. 151. 1827.

Commelina Boucheana R. & S. Syst. 7:1180. 1829.

Commelina pseudo-Zanonia Kunth, Enum. 4:108. 1843.

Commelina mexicana Mart. ex Kunth, loc. cit. 109. 1843.

Commelina glabrata Kunth, loc. cit. 1843.

Tradescantia Gonatandra Schlecht. Linnaea 23:659. 1851.

Gonatandra tradescantioides Schlecht. loc. cit. 1851.

Commelina fastigiata Schlecht. Linnaea 23:188. 1852.

Commelina Hoffmanni Hassk. Ind. Commelin. 80. 1870.

Campeelia Zanonii (L.) HBK. *β. glabrata* (Kunth) C. B. Clarke, in DC. Monogr. 3:315. 1881.

Massive herbs 1–2 m. tall; stems stout, branching rather frequently. Leaves oblong-elliptic to oblanceolate, very narrowly acuminate, gradually narrowed to a subpetiolar base, 10–25 cm. long, glabrous to scatteringly pilose particularly along the margin; sheaths 1–2 cm. long, pilose on the margins. Flowering peduncles lateral, 8–16 cm. long, very slender, simple or branched, usually bearing the sheaths of reduced leaves, glabrous or pilosulose; flowering bracts lanceolate, foliaceous, 2–5 cm. long; umbels bearing few to several rather mediocre white flowers. Sepals 0.5–0.6 cm. long, somewhat foliaceous, glabrous, becoming fleshy and enclosing the fruit at maturity. Petals white, about as long as the sepals.

Mexico to Brazil and Bolivia; Greater Antilles. In wet forests at various elevations.

BOCAS DEL TORO: lower Changuinola River, *Stork 51*; Water Valley, *von Wedel 1540*; Pumpkin River, *von Wedel 2564*; Peach Creek, *von Wedel 2647*. CANAL ZONE: Quebrada Culebra, *Dodge & Allen 17057*; Quebrada Salamanca, *Steyermark & Allen s. n.*; Quebrada Bonita, *Steyermark & Allen s. n.*; Gatún, *Standley 27202*; Barro Colorado Island, *Shattuck 124*. CHIRIQUÍ: El Boquete, *Pittier 2019*; Bajo Chorro, *Woodson & Schery 654*; Quebrada Velo, *Woodson & Schery 252*. COCLÉ: El Valle de Antón, *Woodson & Schery 176*; La Pintada, *Hunter & Allen 634*. DARIÉN: Cana, *Williams 804*. PANAMÁ: Río Tecúmen, *Standley 29361*.

Known popularly as *Conyotura*, *Caña de Cristo*, and *Cañutillo*, and reported as a remedy for venereal diseases. One of the commonest rank herbs of the forests at practically all altitudes.

11. TRADESCANTIA L.

TRADESCANTIA L. Sp. Pl. 411. 1753.

Ephemerum Tourn. ex Moench. Meth. 237. 1794.

Etbeosanthus Raf. Neogenyt. 3. 1825.

Aplopleia Raf. Fl. Tellur. 2:16. 1836 [1837].

Gibasis Raf. loc. cit. 1837.

Phyodina Raf. loc. cit. 1837.

Tropitia Raf. loc. cit. 3:68. 1837.

Heterachthia Kunze, Bot. Zeit. 8:1. 1850.

Mandonia Hassk. Flora 54:260. 1850, non Wedd.

Skofitzia Hassk. & Kanitz. Oester. Bot. Zeitschr. 22:147. 1872.

Small, essentially prostrate subsucculent herbs (in Panama), the stem creeping and ascending at the tips, rooting at the nodes. Leaves alternate, sheathing at the base. Inflorescences subterminal, also lateral at the upper nodes, short- or long-pedunculate, bearing an umbelliform cluster of few to several flowers subtended by 2 conspicuous foliaceous bracts. Sepals 3, free and essentially equal. Petals 3, free and essentially equal. Stamens 6, all fertile and equal. Pistil 3-celled.

Fig. 166. *Tradescantia commelinoides*

1. *TRADESCANTIA COMMELINOIDES* R. & S. Syst. 7:1176. 1829.

Tradescantia commelinoides R. & S. *a. rotundifolia* C. B. Clarke, in DC. Monogr. 3:296. 1881.

Small creeping herbs, the stems ascending at the tips, rooting at the lower nodes, glabrous. Leaves ovate- to oblong-elliptic, acuminate, obtuse and subsessile at the base, 3–8 cm. long, glabrous or ciliate at the base; sheaths 0.5–1.0 cm. long, the margins pilose. Peduncles 1–3 cm. long, usually rather densely pilose; bracts more or less conduplicate, ovate, acute or acuminate, foliaceous, 1.0–2.5 cm. long. Flowers bright pink; pedicels 0.4–0.5 cm. long, minutely puberulent to glabrate; sepals elliptic, keeled, 0.2 cm. long, minutely puberulent; petals 0.5–0.6 cm. long.

Mexico to Panama. In moist high-land forests.

CHIRIQUÍ: Río Chiriquí Viejo valley, Seibert 230; Volcán Chiriquí, Woodson, Allen & Seibert 803; Quebrada Velo, Woodson & Schery 241; Bajo Mona and Quebrada Chiquero, Woodson & Schery 556.

12. ZEBRINA Schnizl.

ZEBRINA Schnizl. Bot. Zeit. 7:870. 1849.

Small creeping, subsucculent herbs; stems slender, ascending at the tips, rooting at the nodes. Leaves alternate, sheathing at the base. Inflorescences terminal, umbelliform, subtended by 2–3 conspicuous foliaceous bracts. Sepals 3, united into a narrow tube, hyaline or scarious. Petals 3, united into a narrow tube, the limb 3-parted. Stamens 6, fertile, essentially equal. Pistil 3-celled.

1. ZEBRINA PENDULA Schnizl. Bot. Zeit. 7:870. 1849.

Cyanotis vittata Lindl. Jour. Roy. Hort. Soc. 5:139. 1850.

Cyanotis Zebrina Nees, Delect. Sem. Hort. Vratislav. 1850.

Small creeping herbs; stems branching frequently, rooting at the nodes, ascending at the flowering tips. Leaves elliptic, acuminate, obtuse and subsessile at the base, 2–6 cm. long, green mottled with silver above, purple beneath, scattering-ly pilose on either surface; sheath 0.5–0.8 cm. long, laxly pilose. Flowering bracts similar to the foliage leaves, subtending an umbelliform cluster of few to

several rather pretty pink flowers. Calyx tube 0.2–0.3 cm. long. Corolla 0.5–0.9 cm. long.

Mexico and Central America, very frequently cultivated, and escaping in warmer climates, the world over. In moist forests at higher elevations.

BOCAS DEL TORO: Water Valley, *von Wedel* 785; Chiriquí Trail, *von Wedel* 2177.

This is the familiar "Wandering Jew" of greenhouses and hanging baskets. Popular names in Costa Rica are reported by Standley as *Hoja de milagro* and *Cañutillo*.

PONTEDERIACEAE

Perennial bog or aquatic herbs with stems and entire leaves. Aerial leaves long-petioled. Stems sometimes reduced. Inflorescence with basal spathe, axillary from the rootstalk or stem; flowers spicate, paniculate or solitary, usually conspicuous, salverform or funnellform, zygomorphic or nearly regular. Calyx and corolla petaloid, marcescent, more or less united. Stamens 3–6, unequally adnate to the perianth tube. Ovary superior; style slender; terminal stigma 3- to 6-lobed or toothed. Fruit an achene or capsule.

- | | |
|---|-----------------|
| a. Stamens 3; perianth nearly regular; flowers solitary or in a few-flowered lax spike; leaf blade relatively small, usually about 1–3 cm. broad..... | 1. HETERANTHERA |
| aa. Stamens 6; perianth zygomorphic; flowers usually many, in large dense spikes; leaf blade relatively large, usually about 4–9 cm. broad. | |
| b. Ovary with 3 fertile cells, ovules numerous in each cell; fruit a dehiscent capsule; flowers relatively large, about 3–6 cm. long; plants floating or more or less rooted and trailing-procumbent; leaves not cordate..... | 2. EICHHORNIA |
| bb. Ovary with 1 fertile cell, ovule solitary; fruit achenoid; flowers smaller, about 1–2 cm. long; plants rooted, erect, or if trailing-procumbent; leaves more or less cordate or sagittate..... | 3. PONTEDERIA |

1. HETERANTHERA R. & P.

HETERANTHERA R. & P. Fl. Peruv. Prodr. 9. 1794; Fl. Peruv. 1:43. 1798.

Phrynium Löfl. Iter Hisp. 178. 1758, as syn.

Schollera Schreb. Gen. 785. 1791.

Heterandra Beauv. Trans. Amer. Phil. Soc. 4:175. 1799.

Leptanthus Michx. Fl. Bor. Am. 1:24. 1803.

Buchosia Vell. Fl. Flum. 33. 1825.

Lunania Raf. Med. Fl. 2:106. 1830.

Triexastema Raf. Fl. Tell. 4:121. 1838.

Plants submerged or floating or of swampy places. Aerial leaves petiolate, expanded; submerged leaves, if present, grass-like. Inflorescence loosely spicate or with a solitary flower. Peduncle exerted from or ensheathed by the spathe. Perianth nearly regular, salverform, white or blue, the outer lobes narrower than the inner. Stamens 3, unequal, one with a much longer filament and larger anther. Ovary many-ovulate. Fruit capsular; seeds very numerous.

- a. Single flower (rarely 2) sub-ensheathed by the spathe; leaves usually dimorphic..... 1. *H. LIMOSA*
- aa. Flowers 2 or many; leaves monomorphic, not grass-like and submerged.
 - b. Leaf blade reniform; inflorescence short-spicate, more or less ensheathed by the spathe; no cleistogamous flowers..... 2. *H. RENIFORMIS*
 - bb. Leaf blade cordate, apex projected; inflorescence long-spicate, not ensheathed by the spathe; lower flowers cleistogamous..... 3. *H. SPICATA*

1. *HETERANTHERA LIMOSA* (Sw.) Willd. Ges. Nat. Freunde Berlin 3:439. 1801.

Pontederia limosa Sw. Prodr. 57. 1788.

Leptanthus ovalis Michx. Fl. Bor. Am. 1:25. 1803.

Heteranthera alismoides Link, Jahrb. Gewachsk. 1³:73. 1820.

Lunania uniflora Raf. Med. Fl. 2:106. 1830.

Triexastema uniflora Raf. Fl. Tell. 4:121. 1838.

Schollera limosa (Sw.) O. Ktze. Rev. Gen. 2:719. 1891.

Phrynium limosum (Sw.) O. Ktze. loc. cit. 3³:318. 1898.



Fig. 167. *Heteranthera limosa*

Rooted plant, sometimes with creeping stems. Leaves usually dimorphic, the submerged linear and grass-like, the aerial with more or less expanded blade lanceolate to oblong, often narrowly so, 1–5 cm. long, base short-cuneate, rounded or shallowly cordate; petiole elongate, stipulate. Spathe sub-ensheathing the inflorescence, caudate, 1.5–4.0 cm. long. Inflorescence of a single flower; flower 2–6 cm. long, tube 1–4 cm. long, blue or whitish; anthers lanceolate, bilobed, almost basifixed; filaments glabrous, adnate to the perianth tube; style elongate, slightly longer than the tube, and with an expanded, tufted stigma. Ovary 1-celled, many-ovulate; capsule oblong, narrow, 1–2 cm. long; seed about 0.4 x 0.8 mm., brown, about 10-ridged longitudinally, one ridge enlarged; seed-coat striated horizontally.

United States to Argentina.

COCLÉ: pools and their margins in wet llanos between Aguadulce and Antón, Woodson, Allen & Seibert 1221. HERRERA: Pesé, Allen 809. PANAMÁ: in pond, vicinity of Bejuco, Woodson, Allen & Seibert 1687; between Panamá and Chepo, Dodge, Hunter, Steyermark & Allen 16720.

2. *HETERANTHERA RENIFORMIS* R. & P. Fl. Peruv. 1:43. 1798.

Heterandra reniformis (R. & P.) Beauv. Trans. Amer. Phil. Soc. 4:175. 1799.

Heteranthera acuta Willd. Ges. Nat. Freunde Berlin 3:438. 1801.

Leptanthus reniformis (R. & P.) Michx. Fl. Bor. Am. 1:25. 1803.

Leptanthus virginicus Pers. Syn. Pl. 1:56. 1805.

Leptanthus peruvianus Pers. loc. cit. 1805.

Heteranthera acuta (Willd.) Vahl, Enum. Pl. 2:42. 1805.

Buchosia aquatica Vell. Fl. Flum. 33. 1825.

Heteranthera virginica (Pers.) Steud. Nomencl. Bot. ed. 2, 2:29. 1841, as syn.

Schollera reniformis (R. & P.) O. Ktze. Rev. Gen. 2:719. 1891.

Phrynium reniforme (R. & P.) O. Ktze. Rev. Gen. 3³:318. 1898.

Plants rooted, with elongate creeping stems. Leaves monomorphic with expanded reniform blade as large as 3 cm. long and 5 cm. broad; petiole extended. Spathe loosely ensheathing, caudate, 1-3 cm. long. Inflorescence short-spicate, 1-5 cm. long, 2- to 6-flowered. Flowers white or lavender, less than 2 cm. long, the tube less than 1 cm. long, usually about 0.7 cm. long; perianth lobes spreading, glandular-pubescent without; anterior sepal reflexed, very narrow; posterior petal somewhat expanded, green at base; stamens dimorphic, anterior longer, about 4 mm. long, posterior ones shorter, about 2 mm. long; larger anther oblong, green, about 1.5 mm. long, smaller ones globular, yellow, basifixed, about 0.5 mm. long; filaments dilated at their base, adnate to the perianth tube; style longer than the tube, about 7 mm. long above the ovary, with an expanded brush-like stigma facing upward and inward. Capsule about 1 cm. long; seed columnar, longitudinally ridged, 0.5-0.8 mm. long, 0.3-0.5 mm. broad.

United States to Argentina.

CANAL ZONE: Summit, Woodson & Schery 1022. CHIRIQUÍ: swamps in pasture, Boquete, alt. 3800 ft., Davidson 571. COCLÉ: bogs, El Valle de Antón, alt. 500-700 m., Seibert 446; between Las Margaritas and El Valle, Woodson, Allen & Seibert 1752; lower Río Antón, Allen 105. BOCAS DEL TORO: Water Valley, von Wedel 1501. PANAMÁ: pool in savanna between Panamá and Chepo, Dodge, Hunter, Steyermark & Allen 16714.

3. *HETERANTHERA SPICATA* Presl, Symb. Bot. 18. 1830.

Schollera spicata (Presl) O. Ktze. Rev. Gen. 2:719. 1891.

Plant rooted in the mud. Leaves erect, long-petioled; blade cordate, 1-6 cm. long and broad, apex acute or obtuse. Spathe 1-3 cm. long, caudate-tipped, ensheathing only the lowest flower. Inflorescence long-spicate, to 10 cm. long, about 10-flowered, the lower 1 to few flowers cleistogamous. Flowers white, about 1 cm. long, the tube 0.3-0.7 cm. long; stamens dimorphic and unequal, larger anther 3 mm. long, the smaller ones 2 mm. long, filaments dilated toward their base, adnate to the tube; style protruding beyond the tube, stigma capitate. Cleistogamous capsules larger than the upper ones, 0.6-1.0 cm. long; seeds ellipsoid, 0.3-0.4 mm. long, 0.2 mm. wide, longitudinally ridged.

Mexico, Panama, Dominican Republic, Cuba.

COCLÉ: Aguadulce, Pittier 4979. HERRERA: Pesé, Allen 808.

2. *EICHHORNIA* Kunth

EICHHORNIA Kunth, Enum. Pl. 4:129. 1843.

Piaropus Raf. Fl. Tell. 2:81. 1837. *Nomen rejiciendum*.

Leptosomus Schlecht. Abh. Nat. Ges. Halle 6:174. 1862.

Cabanisia Kl.; Schlecht. loc. cit. 176. 1862.

Perennial aquatic herbs. Leaves petiolate, blade expanded, petiole often inflated. Inflorescence spicate and with a basal spathe. Perianth showy, 6-parted, somewhat bilabiate, with outer perianth lobes narrower than the inner; upper petal expanded and with yellow spot. Stamens 6, unequal, the 3 shorter included with-

in the throat. Ovary superior, 3-celled, many-ovulate; style elongate; stigma hairy. Fruit a capsule.

- a. Petioles more or less inflated; plant with a short, condensed stem, many roots springing from the base; perianth lobes entire..... 1. *E. CRASSIPES*
- aa. Petioles not inflated; plant with ascending stem, roots often springing from the nodes; margin of perianth lobes erose..... 2. *E. AZUREA*

1. *EICHHORNIA CRASSIPES* (Mart.) Solms in DC. Monogr. 4:527. 1883.

Pontederia crassipes Mart. Nov. Gen. 1:9. 1824.

Pontederia azurea Hook. Bot. Mag. pl. 2932. 1829, excl. syn., not *P. azurea* Sw.

Piaropus crassipes (Mart.) Raf. Fl. Tell. 2:81. 1837.

Piaropus mesomelas Raf. loc. cit. 1837.

Piaropus tricolor Raf. loc. cit. 1837.

Eichhornia speciosa Kunth, Enum. Pl. 4:131. 1843.

Heteranthera formosa Miq. Linnaea 17:61. 1843.

Pontederia elongata Balf. Proc. Bot. Soc. Edinb. 1855:50. 1855.

Eichhornia crassicaulis Schlecht. Abh. Nat. Ges. Halle 6:177. 1862.

Pontederia crassicaulis Schlecht. loc. cit. 1862.

Piaropus crassipes (Mart.) Britton, Ann. N. Y. Acad. 7:241. 1893.

Eichhornia cordifolia Gandoger. Bull. Soc. Bot. Fr. 66:294. 1920.

Floating plants with short, condensed stems and many long, pendant, plumose roots inserted at the stem base; new plants arising through branching and often remaining attached to the parent plant for considerable lengths of time. Leaves with expanded orbicular blades up to 8 cm. broad, and stipulate petioles 2–30 cm. long, petioles excessively inflated in short-petioled leaves, scarcely inflated in very long-petioled leaves. Inflorescence 4–15 cm. long, lightly pubescent with gland-tipped hairs, 4- to 14-flowered. Spathe sub-ensheathing the showy spicate inflorescence. Flowers lavender, 4–6 cm. long, upper petal with a darker purple-blue blotch bearing a yellow spot in the center; tube narrow, about 1.6 cm. long; sepals slightly narrower than the petals; stamens unequal, the 3 longer well exerted, the 3 shorter scarcely extending beyond the tube; filaments glandular-pubescent, adnate to the tube, those of the longer stamens about 2 cm. long, those of the shorter about 0.5 cm. long; anthers linear-oblong, 2-lobed, versatile, about 2.5 mm. long; style elongate with a mop-like capitate stigma. Ovary 3-carpellary, many-ovulate. Seeds 1.2 mm. long, 0.5–0.6 mm. wide.

United States to Paraguay and the Antilles. Naturalized throughout the tropics of the world. The Water Hyacinth multiplies to such an extent that it frequently chokes waterways and becomes a menace to navigation.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 415*. CANAL ZONE: Gatún Lake, *Allen 1965*. CHIRIQUÍ: swamp, Boquete, alt. 3800 ft., *Davidson 613*; *Woodson & Schery 743*.

2. *EICHHORNIA AZUREA* (Sw.) Kunth, Enum. Pl. 4:129. 1843.

Pontederia azurea Sw. Prodr. 57. 1788.

Pontederia aquatica Vell. Fl. Flum. 144. 1825.

Piaropus azureus (Sw.) Raf. Fl. Tell. 2:81. 1837.

Eichhornia aquatica (Vell.) Schlecht. Abh. Nat. Ges. Halle 6:177. 1862.

Plants rooting in the mud or sometimes floating; stems elongate with plumose pendent roots inserted at the nodes. Leaves with orbicular or obovate blades up to 15 cm. broad and fleshy uninflated, stipulate petioles up to 30 cm. long. Spathe

sub-ensheathing the many-flowered spike. Spike 4–15 cm. long with many purplish-blue flowers. Flowers 3.5–5.5 cm. long, the tube about 2 cm. long, glandular-pubescent; perianth lobes spreading, decurrent, erose-margined, 1.5–3.5 cm. long, the upper one with a dark purple base topped by a yellow blotch; petals 3–4 times broader than sepals; stamens unequal, filaments glandular-pubescent, adnate to the tube; stigma red, capitate; style glabrous, about 2 cm. long; ovary 3-carpellary, many-ovulate. Seed 1.0–1.6 mm. long, 0.5–0.8 mm. wide.

Mexico to Argentina and the Antilles.

BOCAS DEL TORO: indefinite, *Cooper* 171. CANAL ZONE: Río Chagres, *Fairchild* 2043; Madden Lake, *Woodson & Schery* 957.

3. PONTEDERIA L.

PONTEDERIA L. Sp. Pl. 288. 1753.

Narukila Adans. Fam. 2:54. 1763.

Unisema Raf. Med. Repos. II. 5:352. 1808.

Perennial marsh or aquatic herbs. Leaves petioled, erect, blade narrow or broad. Inflorescence short or long-spicate, pedunculate, with basal spathe. Spadix and outer perianth more or less hairy, often glandular. Perianth bilabiate, lower 3 segments free, upper 3 adnate for their basal half, middle lobe expanded and with yellow spot. Stamens 6, unequal, posterior 3 included in the throat, filaments adnate toward their base. Ovary with 1 fertile cell containing a single anatropous ovule; style elongate, slender. Fruit achenoid, with persistent style and perianth parts and several protruding or ridge-like crests.

- a. Inflorescence about as broad or broader than long; many rod-shaped glands in hairs at base of the flowers, colorless and inconspicuous in living plants; spathe sub-ensheathing the inflorescence; fruit spiny, appearing bur-like; plant suberect, prostrate-floating, or ascending..... 1. *P. ROTUNDIFOLIA*
- 2a. Inflorescence longer than broad; glands, if present, globular; inflorescence usually well exerted from the spathe; fruit with longitudinal ridge-like crests; plant erect..... 2. *P. CORDATA*



Fig 168
Pontederia rotundifolia

1. PONTEDERIA ROTUNDIFOLIA L. f. Suppl. 192. 1781.

Pontederia cordifolia Mar.; R. & S. Syst. Veg. 7:1142. 1830.

Unisema orbiculata Raf. Med. Fl. 2:108. 1830.

Pontederia eriantha Miq. Linnaea 17:60. 1843.

Plants rooting or creeping in the mud, with stems prostrate-ascending or floating. Leaves (or lower spathe valve) with ovate, sagittate, or reniform-cordate blade, up to 12 cm. long and 18 cm. broad; stipulate petiole up to 25 cm. long, slightly dilated for its lower half. Spathe sub-ensheathing the shortly spicate inflorescence; rachis pilose. Flowers condensed on rachis, 1.7–2.2 cm. long, more or less pilose and light-translucent except for few to many red-brown resin streaks prominent on the expanded perianth segments; tube about 1 cm. long, glandular-pubescent with rod-shaped glands, 2–3 mm. long; upper

corolla lobe expanded and with twin yellow blotches, one on each side of mid-vein (often inconspicuous in fresh flowers), fused toward the base to the adjacent calyx lobes; calyx lobes slightly narrower than the corolla lobes, about 7 mm. long; filaments adnate to the tube at different levels, glandular-pubescent, up to 9 mm. long; anthers narrowly ovate, narrowed toward the apex, 1–1.5 mm. long; fully developed style 1.5 cm. long, with a subcapitate 6-lobed stigma. Fruit ovoid, spiny, about 6–7 mm. long.

Mexico to Uruguay.

CANAL ZONE: Río Chagres near Gamboa, *Allen* 1963; Madden Lake, *Woodson & Schery* 949; Miraflores Lake, *Hunter & Allen* 776.

2. *PONTEDERIA CORDATA* L. Sp. Pl. 288. 1753.

Pontederia angustifolia Pursh, Fl. Am. Sept. 224. 1814.

Narukila cordata (L.) Nieuwl. Am. Midl. Nat. 3:101. 1913.

Unisema cordata (L.) Farwell, Papers Mich. Acad. 3:91. 1924.

Plant erect, emerged, up to 15 dm. tall, rooted in the mud. Petiole elongate, stipulate; leaf blade lanceolate, oblong-lanceolate, cordate, hastate, or sagittate, 3–20 cm. long, 2–15 cm. broad. Spathe loosely ensheathing the lower rachis, with inflorescence usually well exserted; inflorescence longer than broad, 3–13 cm. long; rachis and base of flowers lightly pubescent, sometimes glabrate in age, if glandular-pubescent the glands globular and less than 0.1 mm. in diameter. Flowers white to blue, 8–15 mm. long; tube 5–9 mm. long; stamens unequally adnate to the tube, the 3 lower not exserted beyond the tube; anthers orbicular or oblongoid, about 0.7 mm. long; filaments up to 9 mm. long; style elongate, about 8 mm. long, with a subcapitate, inconspicuously lobed stigma. Fruit oblong-pyriform or ovoid-pyriform, 4–7 mm. long, with longitudinal ridge-like crests.

The familiar Pickerel-weed of the United States and Canada. Three varieties are widespread in the New World tropics; of these only the first enumerated is represented in Panama by existing records, although the two following are also to be expected.

PONTEDERIA CORDATA var. **parviflora** (E. J. Alexander) Schery, comb. nov.

Pontederia parviflora E. J. Alexander, N. Am. Flora 19:1. 1937.

. Leaves almost as broad to half as broad as long, not cordate or only very shallowly so. Inflorescence stocky. Flowers eglandular, 8–12 mm. long, more or less densely villous, hairs with a yellowish cast. Fruit longer than broad, with lacerate crests.

Panama.

COCLÉ: Aguadulce, *Pittier* 4915. HERRERA: Pesé, *Allen* 790. PANAMÁ: swamp on Río Jagua, near El Congor Hill, alt. 2 m., *Hunter & Allen* 466; between Panamá and Chepo, *Woodson, Allen & Seibert* 1661; Dodge, *Hunter, Steyermark & Allen* 16702; Santa María, *Allen* 790.

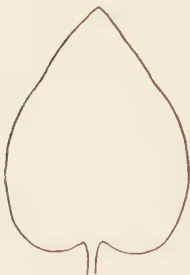


Fig. 169
Pontederia cordata
var. *parviflora*

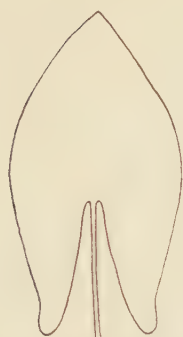


Fig. 170
Pontederia cordata
var. *sagittata*



Fig. 171
Pontederia cordata
var. *lanceolata*

PONTEDERIA CORDATA var. *sagittata* (Presl) Schery, comb. nov.

Pontederia sagittata Presl, Rel. Haenk. 1:116. 1827.

Pontederia cordata f. *sagittata* Solms, in DC. Monogr. 4:533. 1883.

Leaf as broad to half as broad as long, deeply cordate, sagittate or hastate, basal lobes not spreading, nearly parallel. Inflorescence stocky. Flowers usually somewhat glandular at base, slightly villous to glabrate, 8–12 mm. long. Fruit almost as broad or as broad as long, crests scarcely lacerate.

Mexico, Guatemala, Honduras, probably extending to Panama.

PONTEDERIA CORDATA var. *lanceolata* Griseb. Cat. Pl. Cuba. 252. 1866.

? *Unisema sagittata* Raf. Fl. Ludovic. 18. 1817.

Pontederia lanceolata Nutt. Gen. 1:216. 1818.

Pontederia lancifolia Ell. Sketch Bot. S. Car. & Ga. 1:382. 1821, non Muhl.

Pontederia cordata var. *typica* Solms, in DC. Monogr. 4:532. 1883, in part.

Pontederia lanceolata f. *brasiliensis* Fernald, Rhodora 27:81. 1925.

Pontederia lanceolata f. *trullifolia* Fernald, loc. cit. 1925.

Leaf 2–4 times as long as broad, lanceolate, more or less cordate, basal lobes spreading from the petiole. Inflorescence extended, erect. Flowers glandular or hirtellous, 12–16 mm. long. Fruit almost as broad or as broad as long, margins shallowly lacerate.

Mexico to Argentina, but not yet reported from Panama.

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THE DEVELOPMENT AND SYSTEMATIC POSITION OF ARACHNIOTUS TRISPORUS¹

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INTRODUCTION

In 1937 De Lamater described crozier formation in a species of *Arachniotus*, this being the first publication of such a phenomenon in the Gymnoascaceae. The species with which he was working was very similar to *A. aureus*. A year earlier Hotson, in Seattle, Washington, had described a new species of *Arachniotus*, *A. trisporus*, while also in 1936 Vailionis, at Kaunas, Lithuania, described what he thought was a new species, naming it *Gymnoascus sudans*. However, when Vailionis' culture reached the Centraalbureau voor Schimmelcultures, at Baarn, Netherlands, it was identified as *A. trisporus* Hotson. In order to learn whether this species has the same crozier formation as the species of *Arachniotus* with which De Lamater worked we obtained a subculture of Vailionis' strain from Baarn. Upon finding that croziers were produced, a cytological study was made of the organism, as well as a study to determine as clearly as possible its systematic position and its true identity. The results are recorded in the present paper.

HISTORY

The genus *Arachniotus* was created by Schroeter in 1893 to include three species, *A. ruber*, *A. candidus*, and *A. aureus*, the first having been described by Van Tieghem in 1877 as *Gymnoascus ruber* and the other two by Eidam in 1886 as *G. candidus* and *G. aureus*. Schroeter described this new genus as having a globose fruit-body with spherical or ellipsoidal spores, the membranes of which are hyaline, golden, or red. The peridium, the characteristics of which separate this genus from *Gymnoascus*, is composed of uniform hyphae interwoven so as to form a web-like membrane.

¹ An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of master of science in the Henry Shaw School of Botany of Washington University.

Van Tieghem ('77) found *A. ruber* on the dung of the rat and dog. Schroeter ('93) reported finding it on the dung of the dog and goat at Breslau, Germany, and since then it has been found (Masse and Salmon, '02) on cat's dung from Aburi, Gold Coast of Africa. This species differs from the others in having an orange-red or red fruit-body.

Eidam ('86) first found *A. candidus* in Breslau on boiled rice on which he was cultivating *Aspergillus fumigatus*. Schroeter ('93) reported it upon owl's dung in Brieg, Germany. It has also been found (Masse and Salmon, '02) on an old nest of a wild bee and on dung of the common roe, both at Kew, England. The persistent snow-white fruit body and the smooth ascospores are its chief characteristics.

Eidam makes no mention of where he found *A. aureus*, but reports that he repeatedly cultivated it on bread and paper. Schroeter ('93), however, states it was found on decaying vegetables. According to him, it differs from *A. candidus* chiefly by its golden-yellow, minutely spiny ascospores. Another important characteristic is the presence of hyphae in the form of fine spirals.

Masse and Salmon ('02) described a new species, *A. citrinus*, found on the dung of the giant kangaroo in Kew, England. This species resembles *A. aureus* to a great extent, but the color is lemon-yellow rather than golden-yellow, and its ascospores are smooth rather than rough.

Shear, in 1902, described a new species which he called *A. trachyspermus*, associated with diseased cranberries in New Jersey. Like *A. candidus*, it has a white peridium, but its ascospores are echinulate-roughened and show a faint greenish-yellow tint.

In 1936 Hotson found *A. trisporus* in contaminated milk, and Vailionis found the same species (his *Gymnoascus sudans*) as a contamination in a nutrient solution in which he was growing some small branches of birch. According to Hotson, *A. trisporus* differs from other species of genus in the size of the fruit-body, the smooth ascospores, and the three types of spores in its life cycle—ascospores, conidiospores, and chlamydospores. Although the fruit-body is smaller than that reported for *A. candidus*, the two species are very similar, both having smooth ascospores and three types of spores in their life cycle.

MATERIALS AND METHODS

As has been stated, we obtained Vailionis' strain of *Arachniotus trisporus* Hotson from the Centraalbureau voor Schimmelcultures, Baarn, Netherlands, in order to compare it with a known species. This known species was obtained from De Lamater, being a subculture of one which he had received from Baarn and identified by Nannizzi as *A. aureus*. Also, a culture was received from Hotson of his strain of *A. trisporus*.

For general study of the organism, slides were made with Maneval's lactophenol (Maneval, '36) every two or three hours after germination until the time that the ascospores were fully developed from both agar and broth media. For

cytological studies the organism was imbedded in paraffin and stained with Haidenhein's iron-haematoxylin.

For cytological study agar slants in test-tubes proved to be the most adaptable of media. By inoculating many tubes at the same time with spores suspended in sterile distilled water and making slides with lacto-phenol of one tube at regular intervals, it was possible to determine whether the culture was in the desired phase. Killing was accomplished very easily by pouring Gilson's fluid into the test-tube. Flemming's weaker solution was also used, but was not nearly so good as Gilson's for this type of material. The tube containing the fixed material was placed in a water bath into which tap-water was continuously running. The agar slant was removed afterward by gently shaking.

The following schedule was followed for dehydrating:

| | |
|---|--------------|
| Gilson's fluid | 24-48 hrs. |
| Washing | 24 hrs. |
| 5, 10, 20, 35, 50, 70% alcohol | 30 min. each |
| 85% alcohol containing a few drops of iodine ¹ | 2 hrs. |
| 95% alcohol | 30 min. |
| 100% alcohol | Overnight |
| 5, 15, 25, 50, 75% xylol in absolute alcohol | 30 min. each |
| 100% xylol | Overnight |

Imbedded in paraffin 3 days

Sections of 10 μ thickness were quite satisfactory.

The following schedule was followed for staining:

| | |
|---|-------------|
| 100, 66, 33% xylol | 5 min. each |
| 100, 95, 85, 70, 50, 35% alcohol | 5 min. each |
| Wash 10 times over a period of 20 minutes | |
| 4% iron alum | 2 hrs. |
| Wash as before | |
| $\frac{1}{2}$ or $\frac{1}{4}$ % haematoxylin | Overnight |
| Differentiate in 4% iron alum | 1-2 mins. |
| (5 seconds makes a difference) | |
| Wash as before | |
| 35, 50, 70, 85, 95, 100% alcohol | 5 min. each |
| 50, 100% xylol | 5 min. each |
| Mount in balsam | |

Sections were usually counterstained overnight in safranin, erythrosin, or phloxine, dissolved in 50, 70, and 95 per cent alcohol, respectively. A .01 per cent solution of fast green was dissolved in absolute alcohol, and the material immersed in this for one minute only. Germination of spores was studied from slides made with lacto-phenol from spore dilutions at various intervals. For colony studies Petri dishes were inoculated with single spore cultures obtained from making dilution plates of spores. These were incubated, and the colonies measured at regular intervals.

THE ORGANISM

Germination of spores.—The spores of *A. trisporus* germinate usually between 24 and 36 hours after inoculation. The chlamydospores seem to germinate more

¹ Just enough iodine to color is added to prevent precipitation of the mercuric chloride in the material (Kingsbury and Johannsen, '27).

readily than conidia or ascospores. In the process of germination the spore swells to about twice its normal size and at the same time one end of the wall becomes very thin. Soon the wall breaks and the germ-tube appears (pl. 2, fig. 21a, b, f, g). In the ascospore, the tube is produced almost invariably at either of the narrow ends (fig. 21g), and in the chlamydospore at either the blunt or apical end (fig. 21b). When the spore has more than two germ-tubes, they are produced opposite each other as is shown in fig. 21d. The germ-tube, upon lengthening, begins to branch (fig. 21e), but it is still non-septate, except for one septum laid down close to the original spore. After 8 to 10 hours, these branches usually produce immature chlamydospores and conidia which are soon cut off by septa.

Vegetative mycelium.—As Vailionis ('36) has already reported, this organism forms two layers when grown in a liquid nutrient medium, the lower layer being the vegetative mycelium, and the upper the reproductive mycelium. The lower layer is usually imbedded in the medium, whether the latter be a liquid or a solid. If the inoculum is a spore dilution the spores germinate in the liquid and grow immersed for about 72 hours (measuring from the time of inoculation). At about this time the mycelium rises to a position just below the surface where it begins to produce a white compact but fluffy upper layer. The time for the production of this layer varies according to the type of inoculum and the nutrients employed in the medium. If the inoculum is a bit of mycelium, the latter usually floats on the surface, producing the two layers simultaneously. No general statement can be made concerning the nutrients or percentage of nutrients most favorable to growth except that there is great variation. In a solid medium, both layers develop simultaneously, but it is to be noted that the lower layer does not develop as extensively as in a liquid medium, probably due to a lower oxygen tension.

The lower layer consists of simply branched hyphae. The length of the cells may vary, roughly, between 10 and 40 μ , but most frequently between 15 and 20 μ . Vailionis found that the length was about 44 μ . The width of hyphae seems to be more constant than the length. This is usually between 1.0 and 3 μ , although Vailionis found it to be 7.9 μ . The thickness of the hyphae does not necessarily decrease with increase in length. Usually hyphae that increase in length also increase in width and vice versa.

The very young hyphae, i. e., those at 36 to 49 hours (from the time of inoculation), are densely filled with cytoplasm. Vacuoles appear at about 48 hours (pl. 1, fig. 1). Septa, however, usually appear before vacuoles, which become larger and more distinct in ten hours (fig. 2). At about 70 hours more vacuoles have appeared, but they are smaller than previous ones (fig. 3). By 80 hours (fig. 4), the cells have become so vacuolate that the cytoplasm appears to be a fine net and septa are very hard to distinguish although they are most likely still present. In ten more hours the fine reticulation of the cells has been replaced by a very loose network (fig. 5). By the time that ascospores are fully formed, 144 hours, these cells are dead. It can then be said that the vegetative

hyphae pass gradually from a state of dense cytoplasm with definite vacuoles to one of little cytoplasm with indefinite vacuoles.

When the culture is from one to two weeks old, an exudate is produced on top of the mycelium, in the form of small colorless droplets which collect later to form large yellow drops. Vailionis noted this exudate and thought it appropriate to name his new species *Gymnoascus sudans*. From observing the condition of old hyphae and the production of this exudate, the writer has concluded that the latter comes from the vacuoles after the disintegration of old hyphae. De Lamater observed hyphal fusions in his species of *Arachniotus*, but no such phenomenon has been observed in *A. trisporus*.

The vegetative cells are always multinucleate. There does not seem to be any definite number, order, or arrangement (pl. 1, figs. 8-12). Even the size of the nuclei varies as is illustrated. Sometimes it appears, especially in hyphae 48 to 72 hours old, that the nuclei are paired and surrounded by a definite vacuole, but there are so many exceptions that it cannot be said to be a general rule. The writer has not observed any division of nuclei or mitotic figures in the vegetative cells. The nuclei of these hyphae degenerate with the cytoplasm of the cells as is illustrated in pl. 1, fig. 12.

Racquet mycelium.—Racquet mycelium is found in this species as in other species of *Arachniotus*. The cells composing this mycelium are greatly swollen at one end, appearing as clubs attached end to end (pl. 2, figs. 13, 14). They may be greatly distorted as in fig. 13 or hardly discernible from the rest of the hyphae. Hotson ('36) believes that these cells may be food-storage organs. Vailionis ('36) noted them as a characteristic of his species but did not suggest any particular function for them. Nannizzi ('26) pointed out the relationship of the Dermatomyces with *Arachniotus candidus* and with other closely related genera through the presence of this racquet mycelium, as well as other characteristics.

The writer has noted racquet mycelium on all types of nutrients, both solid and liquid. The three cultures of *Arachniotus* were grown on a medium consisting of agar and distilled water in order to see if this type of hypha was produced. It did not appear in either Vailionis' or Hotson's strain of *Arachniotus trisporus*. A few club-shaped cells, however, were observed in Nannizzi's culture, which would seem to indicate that this type of mycelium has nothing to do with food storage as Hotson thought.

Some cells are comparatively short (20 μ) for their width while some may be as long as 60 to 70 μ . Generally, the width varies between 8 and 20 μ . The swelling is usually greater on one side than on the other, and one end is always more densely filled with cytoplasm than the other. Sometimes the cytoplasm shrinks away from the cell wall, causing the latter to wrinkle (pl. 2, fig. 14). Since the racquet mycelium is purely vegetative, it degenerates during the sexual development and is hardly discernible when the ascospores are mature. It can be

concluded from these observations that a racquet mycelium is characteristic of the three strains of *Arachniotus* studied.

Chlamydospores.—The chlamydospores are produced in the upper part of the vegetative layer, as Vailionis ('36) indicates, terminating the ends of short branches. Vailionis reports that they are $8.8\ \mu$ in diameter, but the writer has found that not only do they vary in size but also that they are generally pyriform. The width may range from 4.4 to $8.7\ \mu$, but most often from 6 to $8\ \mu$. The length may be as little as $4.4\ \mu$ and as much as $11.6\ \mu$, but 8 to $10\ \mu$ covers the range in which most of them are found.

The chlamydospore is the first spore to make its appearance in the development of *A. trisporus*, beginning to form almost immediately after the germ-tube has lengthened. Each one is produced on the end of a short branch consisting of one cell, which increases in length as the spore matures (pl. 2, fig. 15). Sometimes, this branch may produce another side-branch below the spore, in which case a cell wall is laid down between the spore and the side branch. The immature spores are non-vacuolate, but as they mature a vacuole makes its appearance (fig. 15b), followed by others. At this time if conditions are favorable (42 to 69 hours) the chlamydospores, instead of forming a heavy cell wall, form an extension of protoplasm at the apical end of the spore (pl. 2, fig. 17). This new growth, a continuation of the hypha on the other end of the cell, results in an intercalary chlamydospore, already noted by Vailionis. It is not uncommon to see that the chlamydospore has sprouted in two places (fig. 16). The hypha produced in such a manner is normal in all respects and may grow to a great length. Sometimes two chlamydospores are found on the same branch separated by only one cell. The occurrence of such a hypha can be explained by the fact that it was produced from the lower chlamydospore and that it in turn produced the terminal chlamydospore.

The several vacuoles in the chlamydospores fuse to form a central one after about 72 hours. The cell wall also begins to thicken at this time (pl. 2, fig. 18). The spore now has usually reached its maximum size and may remain at this size or shrink slightly. As the cell wall becomes thicker, the spore assumes a color between a cream and a cartridge-buff, and may round up as is shown in fig. 19b. The hypha slowly disintegrates, leaving the chlamydospore free.

An examination of the cultures stained with haematoxylin shows that the spores are multinucleate. The number of nuclei is indefinite, and it may vary as much as do those in the cells of the hyphae. The nuclei are situated in the cytoplasm close to the cell wall (pl. 2, fig. 20).

It is evident that the chlamydospores in this organism are produced as an insurance against unfavorable conditions, since they occur only at the beginning of the life cycle and since a large number are produced especially under unfavorable conditions. Hotson ('36) found that the chlamydospores were the only ones to germinate after a period of time. He discovered, in 1925, that it was possible to

obtain transfers from cultures eight years old. By use of Van Teighem cells, he found that the only spores which germinated were chlamydospores. In 1936, he obtained the same results, the original culture being then twenty years old. It has not been possible to test Vailionis' culture but most likely, since the two cultures are quite similar, the results would be the same.

Conidia.—Conidia soon appear in the upper or reproductive layer, after chlamydospores have already begun to form. They are cut off exogenously from a phialide in a manner very similar to that in which conidia are cut off in *Aspergillus* (Thom and Church, '26) and in *Penicillium* (Thom, '30). The phialide is bottle-shaped with a long narrow neck. When a conidium begins to form the apex of the neck swells into a small pyriform, hyaline spore. This is cut off by a cell wall but remains attached to the phialide by the thin and almost invisible cell wall of the latter (pl. 3, fig. 23). A second conidium is formed below the first, and a third below the second, etc., making the first conidium the terminal cell. After the spore has been cut off from the phialide, it continues to grow so that the terminal one is the largest and the others are relatively smaller. The spores are at first densely filled with cytoplasm but as they age a vacuole appears which usually occupies most of the cell (fig. 25). Upon aging the conidium, unlike the chlamydospore, does not secrete a heavy wall but assumes the color of the chlamydospore. The writer's conclusion is that the color of old cultures is due to the color of conidia and of chlamydospores as well as the exudate.

The phialides usually arise in pairs from a cell which may come directly from the vegetative hypha (pl. 3, fig. 27b), or a specialized branch which bears other cells of this type (fig. 27a). Branching is usually dichotomous. This type of conidiophore is strikingly similar to some of those which are produced in *Penicillium*. A comparison of these illustrations with those of Thom ('30) bears out this point. Vacuolation of phialides is relatively constant, and the same for the three strains studied (fig. 23).

The size of conidia is not a constant character, nor could it be considered one as it depends upon their place in the chain, as has already been noted. They may be from 1.5 to 7.3 μ in length and from 0.7 to 4.4 μ in width, but those most commonly observed were 1.5 to 1.9 μ in width and 2.2 to 3.1 μ in length. Vailionis found them to be 5.3 μ in length and 4.4 μ in width.

Vailionis reports that conidia are produced under favorable conditions, but the writer has found that usually they are produced in abundance on agar in which there is no nutrient. They appear in about 18 hours after spore germination and are present in cultures thereafter. Figure 22 of pl. 3 shows a branch of a hypha developing into phialides. Conidia, however, are produced in abundance until copulation begins, a period of 24 hours in normal cultures. Phialides are less in evidence after 78 hours and have disappeared by the time of ascus formation. It is interesting to note that some of the phialides, after producing the spores, proliferate as a regular hypha (fig. 25). This phenomenon has occurred in

Sterigmatocystis auricoma described by Gueguén ('99) and noted by Thom and Church ('26). In this species the secondary sterigmata developed into short hyphae.

An unusual type of phialide and conidium was found on *A. trisporus* produced on oat-meal agar between 60 and 69 hours after inoculation. It occurred only once, and attempts to achieve the same results again were unsuccessful. The phialides were grouped together in such a fashion that from three to five appeared to have arisen from the end of a hypha (pl. 3, fig. 24). Closer inspection showed that the cells supporting the phialides were much reduced, appearing somewhat as in *Penicillium* sect. *Monoverticillata*. Adjacent to these unusual structures was found the common type of conidia as shown in fig. 27. The conidia were much smaller than the ordinary, being $1.3\ \mu$ in length.

It is difficult to determine the number of nuclei in one conidium. The writer has seen spores stained with haematoxylin that show both one and two nuclei in the cell (pl. 3, fig. 26). Whether this is the true state or not could not be determined. It is possible that one nucleus in the apparently uninucleate cells did not stain or that one "nucleus" in the binucleate cells was an artifact.

It is evident from this study that the production of conidia greatly facilitates the spread of this fungus. They are produced in great abundance around the margins of colonies upon aerial hyphae. Theoretically, by this means of reproduction the colony produced from a single spore has the potentiality of continuing growth so long as there is a suitable substratum. The writer has noticed this production of conidia both in a liquid and solid medium.

SEXUAL REPRODUCTION

As the production of conidia declines, sexual reproduction begins. The colony continues reproducing asexually around its margins, while in the center the sexual phase develops. Both Nannizzi ('26) and De Lamater ('37) noted a color change in the mycelium of their species upon the advent of the sexual phase, but we found that *A. trisporus* remains pure white as before. De Lamater also noted that cultures kept in the dark fruit most readily. To test this, six tubes of Sabouraud's agar were inoculated with spores of *A. trisporus*, three placed in the dark and three in the light, and all incubated at approximately the same temperature. It was found that the three in the light developed hyphae from 24 to 48 hours later than those in the dark. After the spores had germinated in the light-exposed tubes, sexuality developed in the normal length of time.

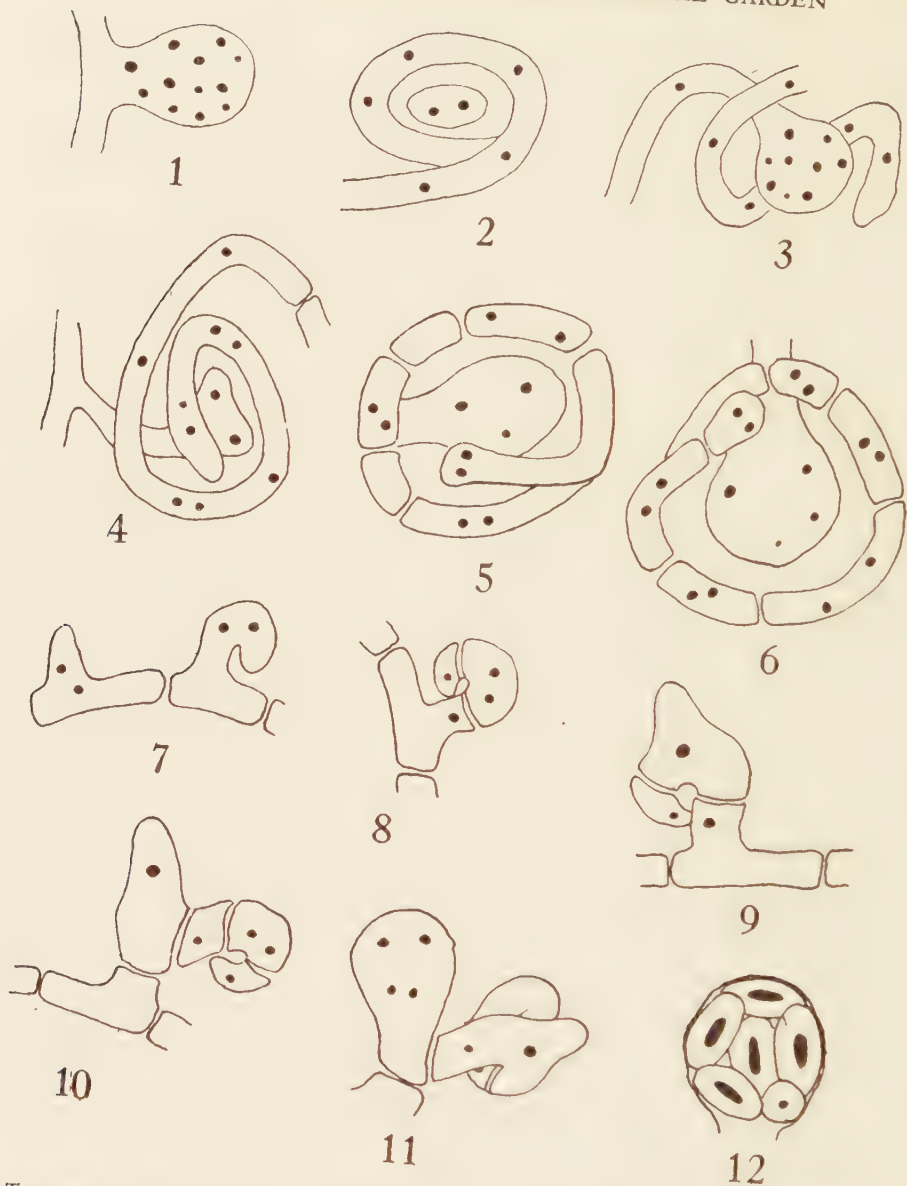
Copulation branches.—The first signs of sexuality are the production of the copulation branches (pl. 4, fig. 28). Baranetzky ('72), who first described *Gymnoascus Reessii* in any detail, a species very similar in development to *Arachniotus trisporus*, designated the male copulation branch as the "sterile cell" and the female as the "ascogene," the latter term from the fact that the branch develops ascogenous hyphae. These arise close to one another, evidently from

vegetative hyphae, but unlike them, are densely filled with cytoplasm. These two copulation branches are not identical in appearance, as were those De Lamater found in his species of *Arachniotus*, but are easily distinguishable by certain characters: (1) The female copulation branch is always longer than the male; (2) it usually becomes septate but the septation is not always evident; (3) the female or terminal cell, which stains very dark, is produced on the end of a fairly long branch (figs. 28b, d, f, and h), while the male cell, which stains just as dark, is produced as a short subterminal branch (figs. 28a, c, e, g). Frequently the male and female copulation branches arise adjacent to each other on the same hypha (fig. 28f and g) but they may be formed separately. Dale ('03) and De Lamater ('37) report the same conditions. Dale, who was working with *Arachniotus candidus*, states that the male branch is first formed and that the female grows around it afterward. In *A. trisporus*, however, the two copulation branches arise simultaneously (figs. 28f, g).

Copulation and fertilization.—The immature copulation branches are not cut off by a septum from the hypha (pl. 4, figs. 28e, f, g). At this time the male and female copulation branches begin to attract each other. Since the female branch is much longer than the male, it is able to draw or to grow towards a male branch and begin to coil around it (fig. 29), whereas the short male branch must remain in its original position. De Lamater states that in his species the two similar branches lying adjacent to each other elongate, swell, and coil up together. It seems that where the two copulation branches are borne close together on the same hypha (figs. 28f, g, and fig. 32) the tendency is for them to repel one another and be attracted by the opposite sex on another hypha. A septum now appears on both branches separating the cells containing the female and male nuclei from the rest of the hyphae (fig. 30). The female copulation branch which has already begun to encircle the male branch forms a tight coil of two or three turns (figs. 30, 31). Several septa have now appeared on the female branch, all formed below the first one (fig. 30). The terminal cell elongates but does not divide. It is this cell which lies adjacent to the male branch in the coil. The male branch elongates but remains unicellular (figs. 31-33). Both the terminal male and female cells are multinucleate (text-figs. 1-3).

Although the writer has not seen the actual movement of the male nuclei to the female branch, she is certain that this must occur. As has been stated, the male copulation cell contains many nuclei which are spaced irregularly. The terminal cell of the female branch is also multinucleate but the nuclei are spaced evenly. Some time later, after the tip of the female branch has come in contact with the male cell (pl. 4, fig. 31), it is found that there are pairs of nuclei evenly spaced in the female branch and that the male branch contains either few or no nuclei. From these observations the writer concludes that the male nuclei migrate into the female branch and pair with the female nuclei.

In this species, copulation and fertilization are much as reported by Dale



Text-fig. 1. Male copulation branch. Fig. 2. Female branch. Fig. 3. The two branches before plasmogamy, and fig. 4, after plasmogamy. Figs. 5 and 6. Septa appearing after nuclei pair in the female branch. Fig. 7. Croziers forming and nuclei migrating into one. Fig. 8. Crozier after nuclei divide and septa are formed. Fig. 9. Beginning of first ascus after fusion of nuclei. Fig. 10. Another crozier forming from fusion of nucleus in tip and stem of crook; note also growth of first ascus. Fig. 11. Third crozier forming from the second, ascus of the second developing, and first divisions of nuclei in first ascus. Fig. 12. Mature ascus showing 6 of the 8 ascospores.

('03) for *A. candidus*. She found that both copulation branches were multinucleate, while De Lamater, working with the species related to *A. aureus*, maintained that they were uninucleate. Both authors agree that a septum separates each copulation branch from the main hypha before fusion of the branches. De Lamater claims that fusion of the two nuclei may occur now or at a much later time, while Dale makes no observations on nuclear fusion.

Formation of croziers.—Soon after fusion of the two copulation branches and the pairing of the nuclei, bulges appear at more or less regular intervals on the outside of the copulation branch, one to each cell (pl. 4, figs. 34-36). These develop into croziers (fig. 37). The two nuclei migrate into the crozier hook and divide in the usual manner (text-fig. 7). Two septa then appear, one cutting off the tip and the other separating the crozier from the female copulation branch (pl. 4, fig. 38, text-fig. 8). The crozier now contains one nucleus at the tip, two at the middle, and one in the main cell. A bulge appears on the outside of the cell containing two nuclei. The nuclei fuse and move into this extension of protoplasm which is the beginning of the ascus (text-fig. 9).

Each cell of the female branch produces more than one crozier in much the same manner as described by Claussen ('12) for *Pyronema confluens*. As the two nuclei in the bend of the hook are fusing the tip of the hook comes in contact with the base and plasmogamy occurs (text-figs. 9, 10). After the fusion of these cells, a crozier is formed into which the nuclei move and divide. Another ascus is now formed, and the process is repeated (text-fig. 11).

De Lamater was the first to describe the formation of croziers in any species of *Arachniotus*. Upon referring to Dale's paper ('03), he found that she had noted the occurrence of "short thick hyphae, which branch repeatedly, and form around the coil a dense mat of ascogenous hyphae." From her illustrations, the "short thick hyphae" are evidently croziers. As croziers occur in *A. trisporus*, it is probable that they are characteristic of this genus.

Ascus formation.—The young uninucleate ascus at first may grow more in length than in width, or it may grow uniformly on all sides. In any case a vacuole appears when the ascus is quite small and enlarges as the ascus does. When almost mature the nucleus, which is situated at the end of the ascus, divides. One daughter nucleus usually migrates to the end of the ascus and the other toward the pedicel. The two nuclei divide perpendicular to the axis of the first division; then these four divide, producing eight nuclei. Cell walls soon appear cutting each nucleus off from the others and forming the ascospores. The vacuole begins to disappear about the time of the second division and is soon lost. The ascus wall is very thin and after the formation of the spores gradually disappears. However, the spores usually adhere together for a long time (pl. 5, fig. 2). The formation of the ascus, particularly as regards the vacuole and the division of the nucleus, according to Dale ('03) and De Lamater ('37), corresponds to that found in *A. trisporus*.

CULTURAL REQUIREMENTS

Arachniotus trisporus grows well upon most liquid or solid media employed for the cultivation of fungi. The solid media found to be successful were: Sabouraud's, potato-dextrose, oat-meal, prune, and Vailionis' agar, as well as potato slants. The species also grew upon corn-meal agar, nutrient gelatin (which it did not liquefy), moist sterile feathers, but not as well on these three media as on those first listed. The most successful liquid media were composed of 1 per cent Bacto-peptone and 2 per cent d-glucose or sucrose. Some growth was also produced on 1 per cent Bacto-peptone and 2 per cent lactose medium.

The following is a "time table" of the development of this organism from the time of inoculation as it occurred upon Sabouraud's, potato-dextrose, and oat-meal agar media. It was used as a standard to compare the development of the organism upon other media.

| | |
|--|--------------|
| Germination of spores..... | 36-44 hrs. |
| Production of chlamydospores..... | 42 hrs. |
| Production of conidia..... | 45 hrs. |
| Production of copulation branches..... | 66-82 hrs. |
| Copulation..... | 69-100 hrs. |
| Formation of croziers..... | 88-124 hrs. |
| Appearance of asci..... | 104-124 hrs. |
| Mature ascospores..... | 124-154 hrs. |

A series of experiments was carried on to determine the effect of various percentages of carbohydrate and peptone upon the growth and structures produced. As a control, the regular 4 per cent d-glucose Sabouraud's agar was employed. The variations with 2 per cent agar were in each case as follows:

"A" medium—2% d-glucose, 1% peptone.

"B" medium—1% d-glucose, 1% peptone.

"C" medium—½% d-glucose, 1% peptone.

"D" medium—2% d-glucose, ½% peptone.

"E" medium—½% d-glucose, .2% peptone.

Slides were made from each of these cultures at 51, 54, 57, 60, 63, 66, 69, 81, 99, 123, and 144 hours after inoculation with lacto-phenol. No variation occurred in structure and amount of chlamydospores, copulation branches, and ascospores which might not occur in the same culture in the same time. The only variation was in Sabouraud's and "A" medium, which at 51 hours had fewer conidia than the others. From these results, it can be concluded that different percentages of d-glucose and peptone had little or no effect upon the size, form, and time of production of the various structures of this organism.

The same percentages of d-glucose and peptone were again employed, without agar, in a liquid medium. The results here are not very reliable because it is difficult to secure a representative portion of one colony in a flask which will correspond to another in another flask. This becomes more and more difficult as the colony increases in size. In making slides as before it was found that at 46 hours, chlamydospores are always produced before conidia. Copulation branches are not produced until at least 96 hours. Croziers appeared at about 144 hours, and mature ascospores were not seen until 200 or more hours. Summarizing these results, it can be said that broth cultures of *A. trisporus* generally

develop more slowly than agar cultures, and also that, for study, agar cultures are much more adaptable than broth cultures.

Since the cultures developed with equal rapidity regardless of the concentration of nutrients, the organism was inoculated on agar containing only d-glucose and on agar containing only Bacto-peptone. The chlamydospores on the d-glucose medium were at first (51 hours) much smaller than usual, being 4.4 to 5.8 μ in diameter. By 67 hours they had become thick-walled, which is also unusual. The ordinary swollen hyphae were evident, but some of the regular hyphae were greatly enlarged. Conidia were as usual. Copulation branches appeared at 90 hours and mature ascospores at 144, which is not unusual. On the peptone media an abundance of conidia was produced throughout the time the slides were made. Chlamydospores were produced but always on very short branches. At 114 hours copulation was observed, but the next two slides, 138 and 152 hours, showed no sexual reproduction at all. It is evident that more work is needed on this problem before any very definite conclusions can be reached. A combination of the two is necessary for normal growth.

Experiments were run to determine the optimum pH. D-glucose, sucrose, and lactose broths were used, and each medium adjusted to pH 6.4, 7.0, and 7.6 as nearly as possible. After the organism had reached maturity, growth was recorded and the pH determined. It was found that growth was good at pH 6.4 and 7.0, and that usually the pH was changed to 6.0 or below. Growth was usually poor at 7.6, and no change of pH was observed.

Upon incubating 18 Petri-dish cultures of *A. trisporus* on Sabouraud's agar, 6 at 24° C., 6 at 30°, and 6 at 35°, the optimum temperature for colony growth was found to be between 30° and 35° C. Cultures inoculated at the same time were again placed in the 30° C. incubator, which ranged from 29° to 31°, and the 35° C. incubator ranging from 33° to 37°. Measured over a period of 70 hours, growth at the lower temperature was spreading and flat, while at the higher temperature an abundance of aerial mycelium as well as concentric rings resulted. Those cultures at 30° C. were 0.4 cm. larger than those at 35° C. It can be concluded, then, that the optimum temperature is between 30° and 35° C., most likely 33° C.

PATHOGENICITY

The writer, upon accidentally pricking her finger with a contaminated needle, found that after 48 hours a small vesicle appeared. To confirm the suspicion that this was caused by *A. trisporus*, with aseptic precautions she inoculated a portion of the skin of the arm with spores of this organism. After a period of 48 hours it was evident that the fungus was maintaining itself satisfactorily enough to exist but not to grow to any extent. A small raised slightly inflamed spot on the arm was the only indication of the organism. At the end of three weeks, the lesion was opened aseptically, and some of the tissue placed upon a sterile Sabouraud's agar plate. Within 48 hours, the organism germinated and

grew as usual. The experimental lesions healed spontaneously in about a week. This is the first record of the pathogenicity of any species of *Arachniotus*, to the writer's knowledge. It is interesting to note that it is possible for this fungus to live pathogenetically, and that it certainly causes no serious harm.

IDENTIFICATION

There is no doubt that the species in question is a member of the genus *Arachniotus*. It possesses the characteristics which Schroeter ('93) lists for the genus, namely, a globose fruit-body of interwoven hyphae resembling a spider web, and spherical or ellipsoidal spores, the membranes of which are either hyaline, golden, or red. It cannot be placed in closely related genera, such as *Gymnoascus*, because of the absence of spines on the hyphae of the peridium, nor in *Amauroascus*, because of the brown peridium, nor in *Ctenomyces*, because of the well-developed peridium and the comb-like appendages. Plate 5, fig. 2, illustrates the loose non-appendaged peridium of *A. trisporus*.

In determining the true species, the characteristics of all species known will be listed. They are as follows:

ARACHNIOTUS RUBER Schroet. in Cohn, Krypt. Fl. Schles. 3²:211. 1893.

Gymnoascus ruber Van Tiegh., Bull. Soc. Bot. France 24:159. 1877.

Fruit-body orange-red or red, 0.5 mm. in diameter at the most; ascospores orange-red or red, $4.5 \times 3.5 \mu$; only 6 to 20 asci per perithecium, fewer than in other species. Isolated from dung of dog, rat and goat at Breslau; from cat's dung, Aburi, Gold Coast.

ARACHNIOTUS CANDIDUS Schroet. in Cohn, Krypt. Fl. Schles. 3²:210. 1893.

Gymnoascus candidus Eidam, Schles. Ges. Vaterl. Kultur, Ber. Bot. Sect. 160-165. 1886.

Fruit-body snow-white, globose, 0.5-2 mm. in diam.; ascospores hyaline, ellipsoidal, smooth, $3.5 \times 3 \mu$; conidia pyriform, in chains (fide Schroeter, none reported by Eidam, probably the oidia of Dale and aleurospores of Nannizzi). Isolated from boiled rice, owl's dung in Brieg, old nest of wild bee and dung of common roe at Kew, England.

ARACHNIOTUS AUREUS Schroet. in Cohn, Krypt. Fl. Schles. 3²:210. 1893.

Gymnoascus aureus Eidam, Schles. Ges. Vaterl. Kultur, Ber. Bot. Sect. 160-165. 1886.

Fruit-body golden-yellow, 0.5-1 mm. in diam.; with fine hyphal spirals in the peridium; ascospores golden-yellow, spherical to ellipsoidal, spiny, $3.5-4.0 \mu$ in diam.; conidia not reported by Schroeter, aleurospores by Nannizzi. Isolated from decaying vegetables.

ARACHNIOTUS CITRINUS Massee & Salm., Ann. Bot. 16:62. 1902.

Fruit-body lemon-yellow; ascospores ovoid to subglobose, smooth, $4-5 \times 2.5-3.5 \mu$; conidia not reported. Isolated from dung of giant kangaroo, Kew, England.

ARACHNIOTUS TRACHYSPERMUS Shear, Science, N. S. 16:138. 1902.

Fruit-body white; ascospores faintly greenish-yellow, echinulate, $3.25-4.0 \times$

2.0–2.5 μ ; conidia resembling those of *Penicillium*. Isolated from diseased cranberries.

ARACHNIOTUS TRISPORUS Hotson, *Mycologia* 28:497-500. 1936.

Fruit-body white, turning yellowish with age, 160–326 μ in diam.; asci ellipsoidal to spherical, 7–9 x 10–11 μ ; ascospores hyaline, ellipsoidal, smooth, 3.5 x 5.5 μ ; conidia hyaline, ellipsoidal, 3.5–4.5 x 4.5–5.5 μ ; chlamydo-spores sub-spherical to pyriform, 6–7 x 7–11 μ . Isolated from contaminated milk.

GYMNOASCUS SUDANS Vailionis, Vyt. Didžiojo Univ. Mat.-Gamtos. Fak. Darbai 11:119. 1936.

Fruit-body white; asci spherical to pyriform, 13.2 μ in diam.; ascospores hyaline, ellipsoidal, smooth, 8.8 x 6.6 μ ; conidia hyaline, ellipsoidal, 5.3 x 4.4 μ ; chlamydo-spores spherical to pyriform, hyaline, 8.8 μ . Isolated from a nutrient solution in which birch twigs were being cultivated.

GYMNOASCUS SUDANS Vailionis (description based on subculture of Vailionis' original culture).

Fruit-body white turning to cartridge-buff upon aging, size variable; asci ellipsoidal to spherical, 7.3–7.5 x 10.2–10.6 μ ; ascospores hyaline, ellipsoid, smooth, 3.1–3.3 x 4.3–4.6 μ ; conidia hyaline to cartridge-buff, pyriform, 1.5–1.9 x 2.2–3.1 μ ; chlamydo-spores cartridge-buff, pyriform, 6–8 x 8–10 μ .

Of the above species, it is possible to place Vailionis' organism under *Arachniotus trisporus*, as has been previously done, or under *A. candidus*. It being impossible to obtain a culture of *A. candidus* it is necessary to rely strictly upon the literature, which is certainly not complete and quite contradictory. Since the size of the ascospores of that species differs slightly from that of *A. trisporus*, the description of conidia conflicting, and since no mention is made of chlamydo-spores, exudate, or the color upon aging, the writer must conclude that to call this species *A. trisporus* is justifiable. Furthermore, it being impossible at the present time to determine the month in which Vailionis published his description, and since his organism is already known as *A. trisporus*, we believe that it should continue to be known under that name.

Since Vailionis discovered his species in Lithuania and Hotson his in the state of Washington, it was thought that some difference must occur between the two cultures. However, after a microscopical study of the two, their morphological structures were found to be identical in size and relative abundance. Colony characteristics, however, were slightly different (pl. 6). The cultures were then designated as Vailionis' strain and Hotson's strain.

After making a thorough study of the culture identified by Nannizzi as *A. aureus*, obtained from Baarn through De Lamater, the writer concluded that this organism was of the same species but a different strain from the other two. Its colony characteristics (pl. 6) are different from the others, but the color of the mycelium, the exudate, and its morphological characters are identical. For these reasons the writer designates this culture as *A. trisporus*, Nannizzi's strain.

SYSTEMATIC POSITION OF ARACHNIOTUS

Arachniotus occupies a position between the Gymnoascaceae and the Aspergilliaceae, because it has a loosely woven peridium as found in the former, and conidia resembling very strongly those found in the latter. It should be considered as one of the lowest members of the family Gymnoascaceae, since there are only traces of a peridium the hyphae of which are undifferentiated. It is the only known member of this family showing crozier formation and, according to De Lamater, the most primitive fungus having croziers. The presence of conidia in *Arachniotus*, produced from such similar structures as found in *Aspergillus* and *Penicillium* and also in a similar fashion, supplies a strong link to bridge the gap between the Gymnoascaceae and the Aspergilliaceae.

It has long been thought that the Trichophytoneae or the Dermatophytes were imperfect forms of the Gymnoascaceae. (For a review of the literature pertaining to this subject, see Dodge, '35). However, definite proof of this relationship has not as yet been established. Pollacci ('25) stated that when *A. candidus* is cultivated on Pollacci agar perithecia do not develop and that the organism closely resembles *Trichophyton*. Nannizzi ('26) cultivated *T. radiolatum*, *T. asteroides*, *T. denticulatum*, and *T. felineum* upon feathers, skin, leather, and bones, and found that they produced pycnidia resembling the ascocarps of *Ctenomyces serratus*, *Arachniotus candidus*, *A. aurcus*, and *Gymnoascus Reessii*, which he also studied. In this paper he brought out, besides other morphological similarities, the significance of finding the racquet mycelium in *Microsporon* and in *Ctenomyces serratus* and *Myxotrichum uncinatum*. Although the writer was unable to make such a study as Nannizzi did, she believes that the presence of the racquet mycelium in the perfect and imperfect forms is a morphological connection between these two groups. Nannizzi has shown in his figures that *Ctenomyces serratus*, *Myxotrichum uncinatum*, *Microsporon lanosum*, and *Trichophyton radiolatum* (to some extent) all possess racquet mycelium. Illustrations in Ota and Langeron ('23) show that *Microsporon Audouini*, *Megatrichophyton equinum*, *M. ferrugineum*, and *Favotrichum ochraceum* possess similar mycelium.

From the above, three significant findings should be brought out: First, racquet mycelium occurs almost invariably in all three strains of *A. trisporus*. Second, *A. trisporus* has an optimum growth temperature between 30 and 35° C., a range at which most of the Dermatophytes grow the best. Third, and one of the most important, *A. trisporus* can definitely exist as a parasite. These three facts all point towards the conclusion that the Trichophytoneae are the imperfect forms of the Gymnoascaceae, but unfortunately does not finally establish this theory as a fact.

SUMMARY

1. *Arachniotus trisporus*, besides having regular multinucleate hyphae of a more or less constant width and length, is characterized by a racquet mycelium similar to that found in the Gymnoascaceae and the Trichophytoneae.

2. *A. trisporus* reproduces asexually by multinucleate chlamydospores and uni- or binucleate conidia. The chlamydospores have proved to be the most viable type of spore over a period of years. The conidia are produced in chains from a phialide as in the *Aspergillaceae*.

3. In sexual reproduction, two unlike multinucleate copulation branches are produced which, after copulating, fuse. The male nuclei move into the female branch and the nuclei pair. Cell walls appear between each pair, and croziers are formed. The two nuclei in the tip of the crozier fuse and divide three times, producing eight uninucleate ascospores. The ascus wall soon disappears but the ascospores usually remain clumped together as they appeared in the ascus.

4. This species is capable of good growth upon Sabouraud's, potato-dextrose, oat-meal, prune, and Vailionis' agar. Growth in liquid media of the same composition, but without the agar, is good, but the development of the organism is slower. A "time table" of the appearance of the various morphological structures is given. It is found that the optimum pH is near 6, and that the optimum temperature is between 30° and 35° C.

5. *Gymnoascus sudans* Vailionis is identical with *A. trisporus* Hotson.

6. This species is capable of existing as a pathogen.

7. Because of the presence of a loose undifferentiated peridium, *A. trisporus* belongs in the *Gymnoascaceae*, but, on the other hand, it produces conidia similar to those found in the *Aspergillaceae*. It is therefore believed that this organism occupies a position between the two families.

8. The presence of a racquet mycelium in *A. trisporus*, similar to *Ctenomyces* and *Myxotrichum*, and also species in the *Trichophytoneae*, suggests that the *Trichophytoneae* are related to the *Gymnoascaceae*. Besides the presence of a racquet mycelium, the optimum temperature of 30° and 35° C. and the demonstration of the pathogenicity of this species also point in this direction.

ACKNOWLEDGMENTS

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EXPLANATION OF PLATE

PLATE 1

Arachniotus trisporus

Figs. 1-6. Vegetative hyphae from lacto-phenol prepared slides from potato-dextrose agar cultures, showing development of the vacuole from time of inoculation. Width of hyphae shown is 2.5 μ .

Fig. 1, after 51 hours.

Fig. 2, after 60 hours.

Fig. 3, after 69 hours.

Fig. 4, after 81 hours.

Fig. 5, after 99 hours.

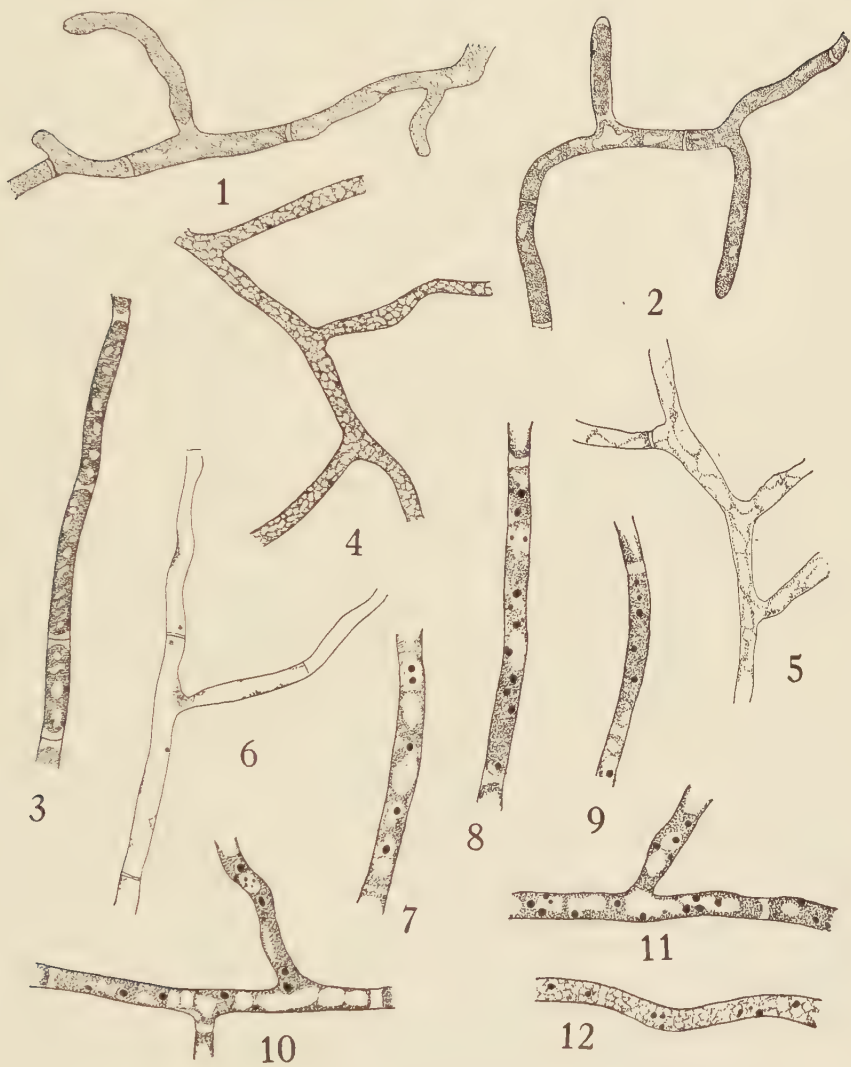
Fig. 6, after 144 hours.

Figs. 7-12. Vegetative hyphae from iron-haematoxylin prepared slides showing nuclei and development of the vacuole from time of inoculation.

Figs. 7-9. Hyphae 2.5 μ in width, from 52-hour potato-dextrose agar cultures.

Figs. 10-11. Hyphae 2.5 μ in width from 60-hour Sabouraud's agar culture.

Fig. 12. Hyphae 2.2 μ in width from 81-hour potato-dextrose agar culture.



ROSENBAUM—ARACHNIOTUS TRISPORUS

EXPLANATION OF PLATE

PLATE 2

Arachniotus trisporus

Figs. 13-14. Portion of racquet mycelium at 57 hours taken from lacto-phenol prepared slides made from potato-dextrose agar cultures:

Fig. 13. Cell marked *a* is $10\ \mu$ at widest part and $54.5\ \mu$ long.

Fig. 14. Cell marked *a* is $15.5\ \mu$ at widest part and $43.7\ \mu$ long.

Figs. 15-21. Chlamydospores and germinating spores taken from lacto-phenol prepared slides except fig. 20, which is from an iron-haematoxylin preparation.

Fig. 15. From a 51-hour oat-meal agar culture: *a*, $5.6 \times 7.5\ \mu$; *b*, $4.4 \times 4.4\ \mu$; *c*, $5.0 \times 5.6\ \mu$.

Fig. 16. From a 48-hour potato-dextrose culture, showing continuation of hyphae from apical end of spore: spore $10.0 \times 11.3\ \mu$.

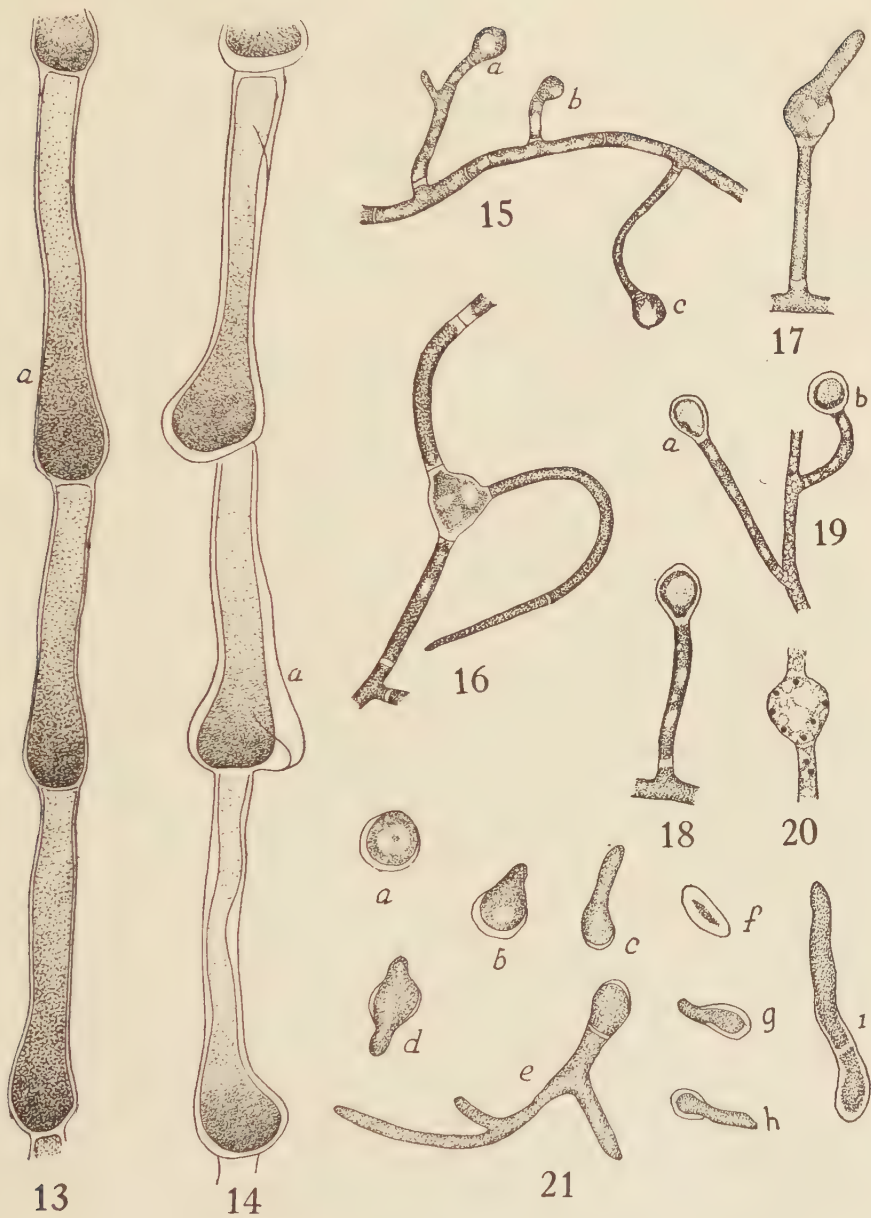
Fig. 17. Sprouting chlamydospore from a 45-hour potato-dextrose culture: spore $8.8 \times 10.0\ \mu$; projection $10\ \mu$ long.

Fig. 18. From a 78-hour oat-meal agar culture; chlamydospore $8.8 \times 9.4\ \mu$.

Fig. 19. From a 94-hour Sabouraud's agar culture: *a*, $8.1 \times 5.6\ \mu$; *b*, $6.2 \times 6.2\ \mu$.

Fig. 20. Showing nuclei from a 46-hour culture.

Fig. 21. *a*, *b*, *c*, *d*, and *e*, germinating chlamydospores; *f*, *g*, *b*, *i*, germinating ascospores.



ROSENBAUM—ARACHNIOTUS TRISPORUS

EXPLANATION OF PLATE

PLATE 3

Arachniotus trisporus

Illustrations of conidia, all taken from lacto-phenol prepared slides except fig. 26.

Fig. 22. Immature conidia taken from a 51-hour culture; hypha 1.3 μ in width; terminal spore 2.5 μ in diameter.

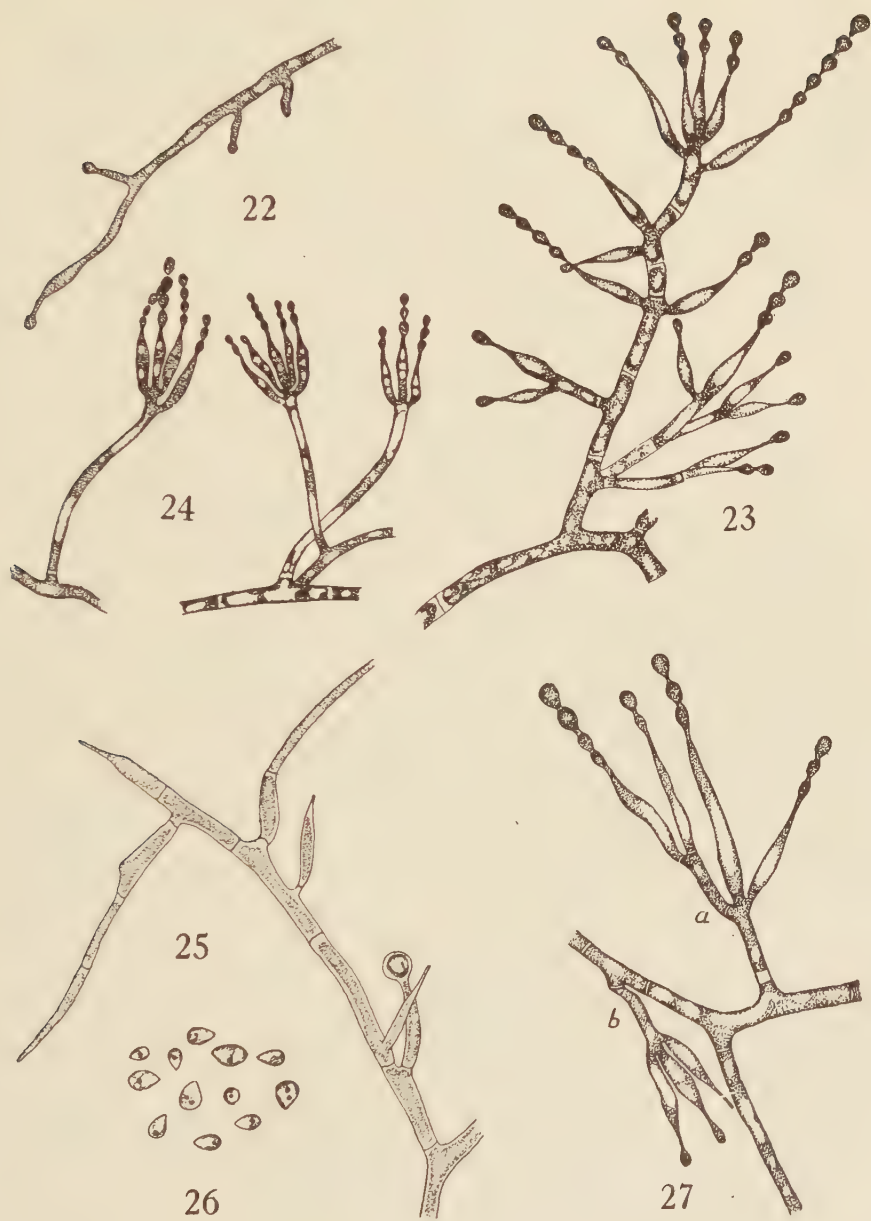
Fig. 23. Branch of conidia taken from a 54-hour oat-meal agar culture.

Fig. 24. An unique type of conidium produced on oat-meal agar between 61 and 69 hours.

Fig. 25. Phialides, after the production of conidia, continuing growth as hyphae; taken from an 81-hour culture.

Fig. 26. Conidia stained with iron-haematoxylin showing some with one, and some with two nuclei.

Fig. 27. Conidia from a 54-hour culture.



ROSENBAUM—ARACHNIOTUS TRISPORUS

EXPLANATION OF PLATE

PLATE 4

Arachniotus trisporus

Illustrating copulation branches, copulation, and formation of croziers, taken from lacto-phenol prepared slides.

Fig. 28. Copulation branches from a 98-hour potato-dextrose agar culture; *a*, *c*, *e*, and *g* are male, while *b*, *d*, *f*, and *h* are female copulation branches.

Fig. 29. Female copulation branch drawing toward male.

Fig. 30. Female branch coiling around the male; meanwhile the tip of each branch has been cut off by a septum.

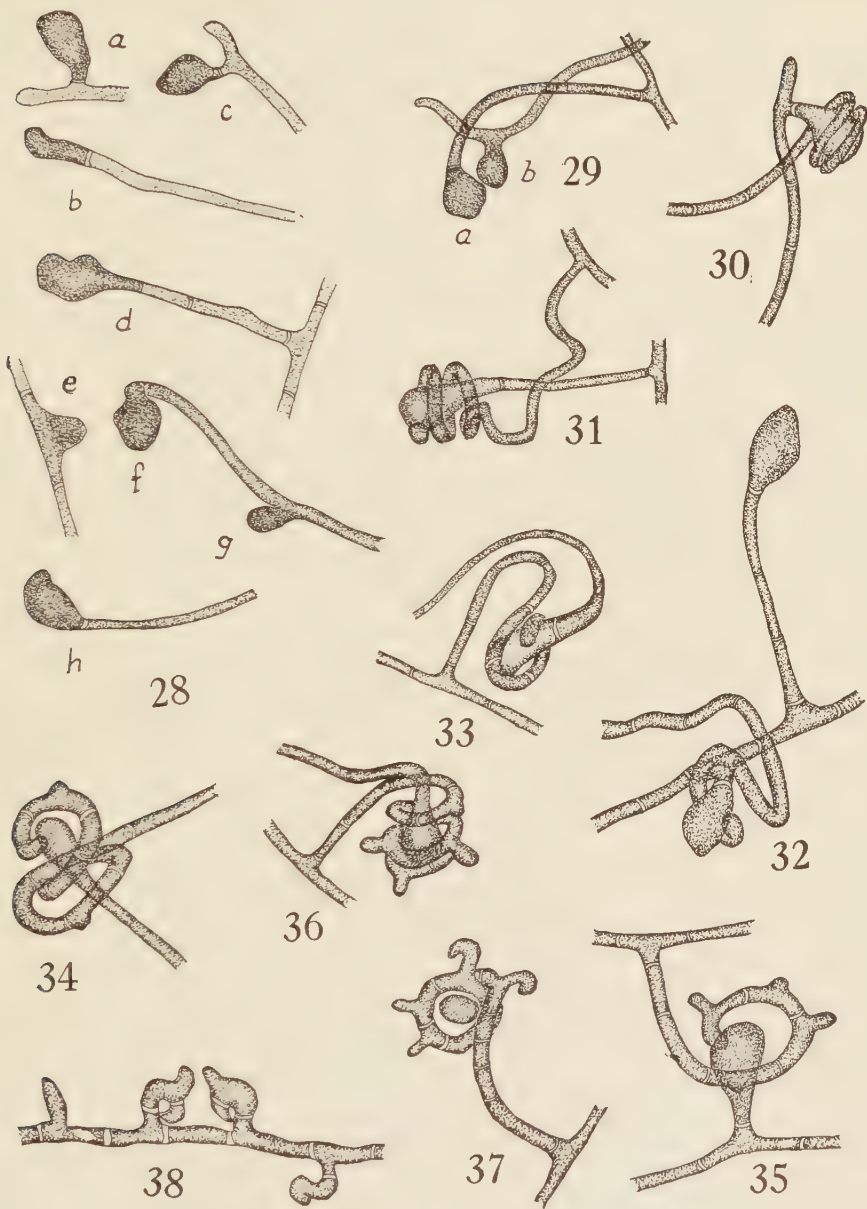
Fig. 31. Copulation of the male and female branches, showing the septa that have appeared before the first septum in the female copulation branch.

Fig. 32. Illustrating the attraction of a female branch from another hypha to the male, and repulsion of the adjacent female branch.

Fig. 33. Septa appearing in the female branch after plasmogamy has taken place.

Figs. 34–37. Various steps in the formation of croziers after septa have divided the female branch into several cells.

Fig. 38. Portion of original female copulation branch showing mature croziers which have begun to form asci.



ROSENBAUM—ARACHNIOTUS TRISPORUS

EXPLANATION OF PLATE

PLATE 5

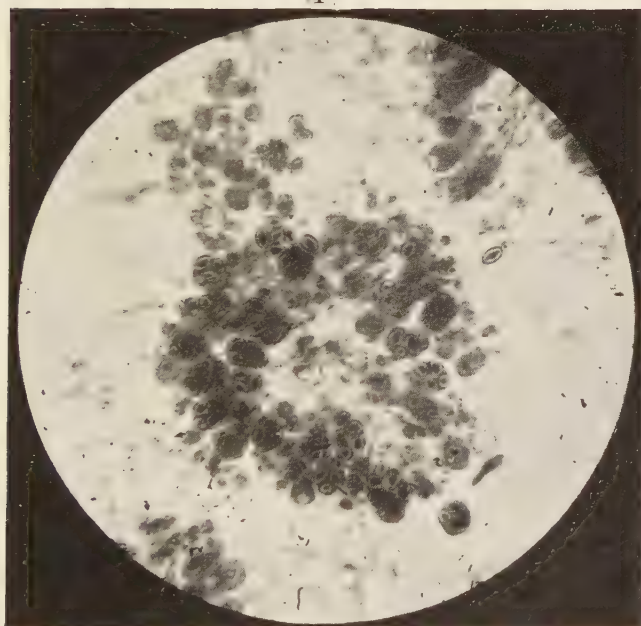
Arachniotus trisporus

Fig. 1. Photomicrograph of vegetative hyphae, showing copulation branches at the extreme ends (x approx. 360).

Fig. 2. Photomicrograph of a fruit-body, showing asci and ascospores (x approx. 745).



1



2

ROSENBAUM—ARACHNIOTUS TRISPORUS

EXPLANATION OF PLATE

PLATE 6

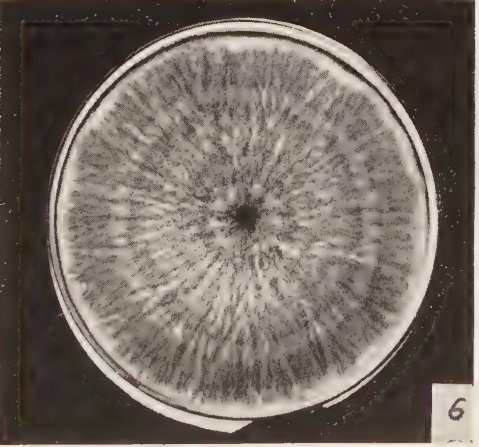
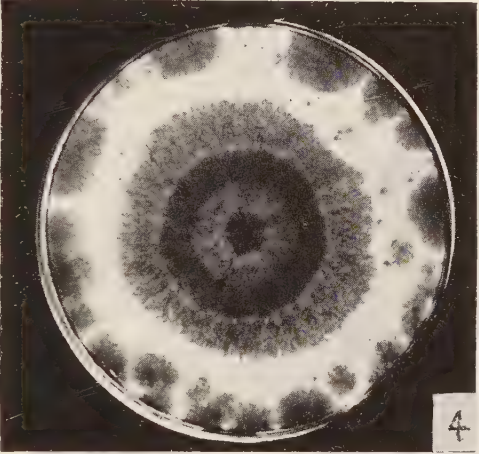
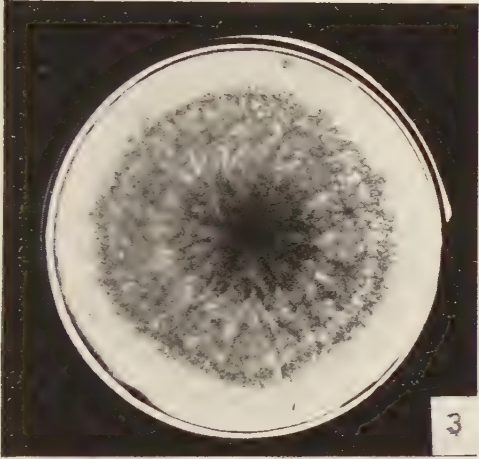
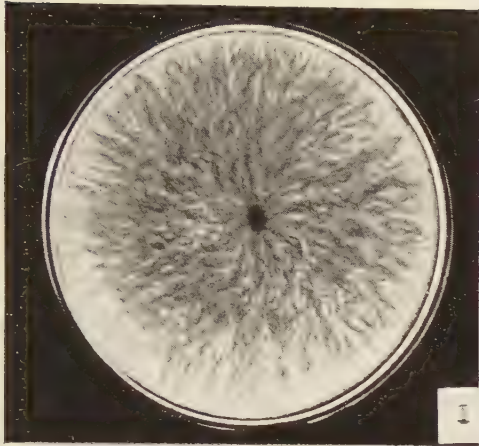
Arachniotus trisporus

Photographs of Petri-dish cultures of the three strains grown on Sabouraud's agar. Figs. 1, 3, and 5 were incubated at approximately 30° C., and figs. 2, 4, and 6, at approximately 35° C. Note the formation of rings when grown at 35° C.

Figs. 1 and 2. Vailionis' strain.

Figs. 3 and 4. Nannizzi's strain.

Figs. 5 and 6. Hotson's strain.



ROSENBAUM—ARACHNIOTUS TRISPORUS

INSTABILITY OF THE MATING TYPE ALLELES IN SACCHAROMYCES¹

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COMPLETE TRANSFORMATION OF SACCHAROMYCES INTO TORULAE

Copulation in *Saccharomyces cerevisiae* is controlled by a pair of *a/a* alleles. Ascospores are haploid for either the *a* or the *α* gene and produce clones, the members of which copulate pairwise when the cultures are mixed. The *a* by *a* matings result in abundant copulations, forming legitimate diploid zygotes capable of undergoing reduction to produce viable 4-spored asci. The *a* by *α* and the *α* by *a* matings fail to result in copulations. The four cultures from the single haploid ascospores which were the basis of the experiments and illustrations in our earlier papers (Lindgren and Lindgren, '43 b, c) have been carried in culture in the laboratory for over a year and have been observed to produce a great variety of morphological mutants. That they still retain their haploid character is shown by the shape and size of the cells. Recently the earlier experiments were duplicated by mating the cultures in all possible pairs, following exactly the same procedure as before. These matings failed to produce either copulations or diploid cells. No asci were obtained by transferring the mated cultures to our presporulation medium and gypsum slants (Lindgren and Lindgren, '44). The cultures are now completely neutralized as to sex and have been transformed into typical members of the genus *Torula* or *Torulopsis*. They are incapable of producing diploid sporulating cultures either by legitimate or illegitimate copulation. This is undoubtedly due to mutation either of the principal *a/a* alleles or of modifying genes which inhibit copulation.

The genus *Torula* or *Torulopsis* was invalidated by Šatava ('34) and Winge and Laustsen ('39) suggested that the genus *Zygosaccharomyces* should be dropped. We have presented evidence on both these points ('43b), and the names of the genera are used in the present discussion without implication of generic status.

THE EFFECT OF CAMPHOR ON COPULATION

Thaysen and Morris ('44) produced large, presumably diploid cells of *Torula utilis* by plating the organisms on beer wort agar containing 0.3 per cent camphor. We tested the effect of camphor on a number of yeast cultures and found that with concentrations of 0.3 per cent camphor about half of the cultures produced outgrowths strongly resembling copulation tubes; and with 0.5 per cent camphor a much larger proportion of cultures produced an abundance of these structures.

¹ This work was supported by a grant from Anheuser-Busch, Inc., St. Louis.

Plate 7 shows the effect of 0.3 per cent camphor on a diploid and a haploid culture.

The fact that camphor stimulates the production of structures resembling copulation tubes suggested that Thaysen and Morris had been able to produce a large *Torula* by inducing copulation between normally stable haploid cells and led to the following experiment. The four single ascospore cultures, referred to above, which had become transformed into *Torulæ*, were mated in all combinations in malt-dextrose-yeast extract broth containing 0.5 per cent camphor and compared with a control in which matings were made in the absence of camphor. In the presence of camphor many tubes grew out and anastomoses were visible between adjacent cells. Cells from each copulating culture were transferred to our presporulation medium and then to gypsum slants. No diploid cells or spores were obtained as a result of the above matings, either with or without camphor, indicating that in spite of the abundant production of tubes none of the cell fusions had been followed by nuclear fusion.

This first failure to effect nuclear fusion by the use of camphor was followed by a second experiment with fresher cultures. Four cultures, which had been obtained from four single ascospores of a single ascus about six months before, were similarly mated in the presence and absence of camphor. The serial numbers of these four cultures are 61, 62, 63, and 64. Cultures 61 and 62 are typically round-celled, while 63 and 64 are somewhat ellipsoidal. Earlier tests had shown that 61 and 62 were of the same mating type, while 63 and 64 were of the opposite. Outline drawings of the cells mated in broth without camphor are shown in fig. 1. Originally the cells of 63 and 64 were about the same size but some of those of culture 63 are seen to be much larger than the standard haploid ones and are characteristically diploid, indicating that this culture had become diploid spontaneously by illegitimate copulation. This culture, therefore, contains a mixture of haploid and diploid cells.

The results of the pairings shown in fig. 1 indicate that copulations failed to occur when cultures 61 and 62 were mated, and also with 63 and 64, but copulations occurred in the other four possible combinations. This proves that the four cultures still retain the same mating type differences which had characterized them in the previous experiments. It is probable that only the haploid cells in culture 63 mated, but it would require further analysis to determine this specifically.

Cells from the culture tubes in which the matings were made were transferred to our presporulation medium and, after the proper interval, were placed on gypsum slants. The photographs in pl. 8 show the ascospores obtained on gypsum slants, and confirm the findings of the previous matings. Cultures 61, 62, and 64 produced no ascospores; culture 63, however, which had contained illegitimate diploids, developed a few ascospores. Many of these were characteristically aborted and most of them were probably non-viable. This culture is unusual for an illegitimate diploid inasmuch as it produces a relatively large

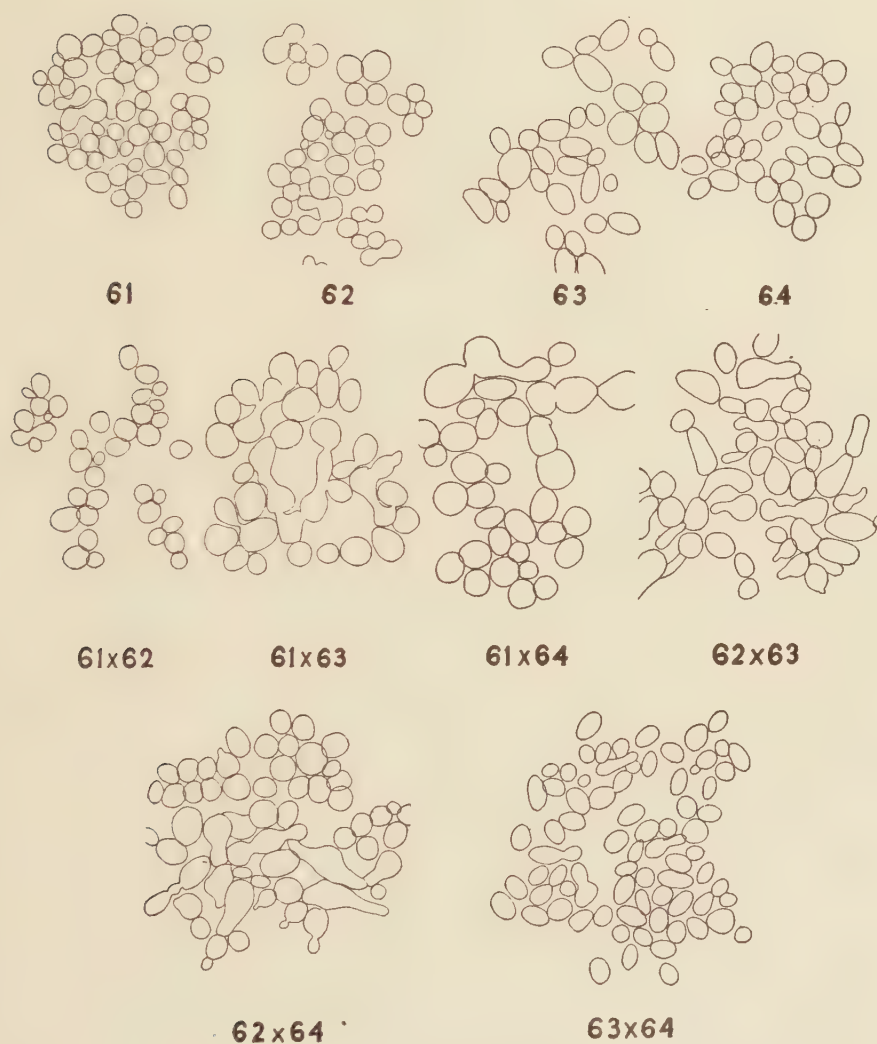


Fig. 1. Outline drawings of the cells of cultures 61, 62, 63, and 64, and all possible pairings from mating tubes in broth without camphor.

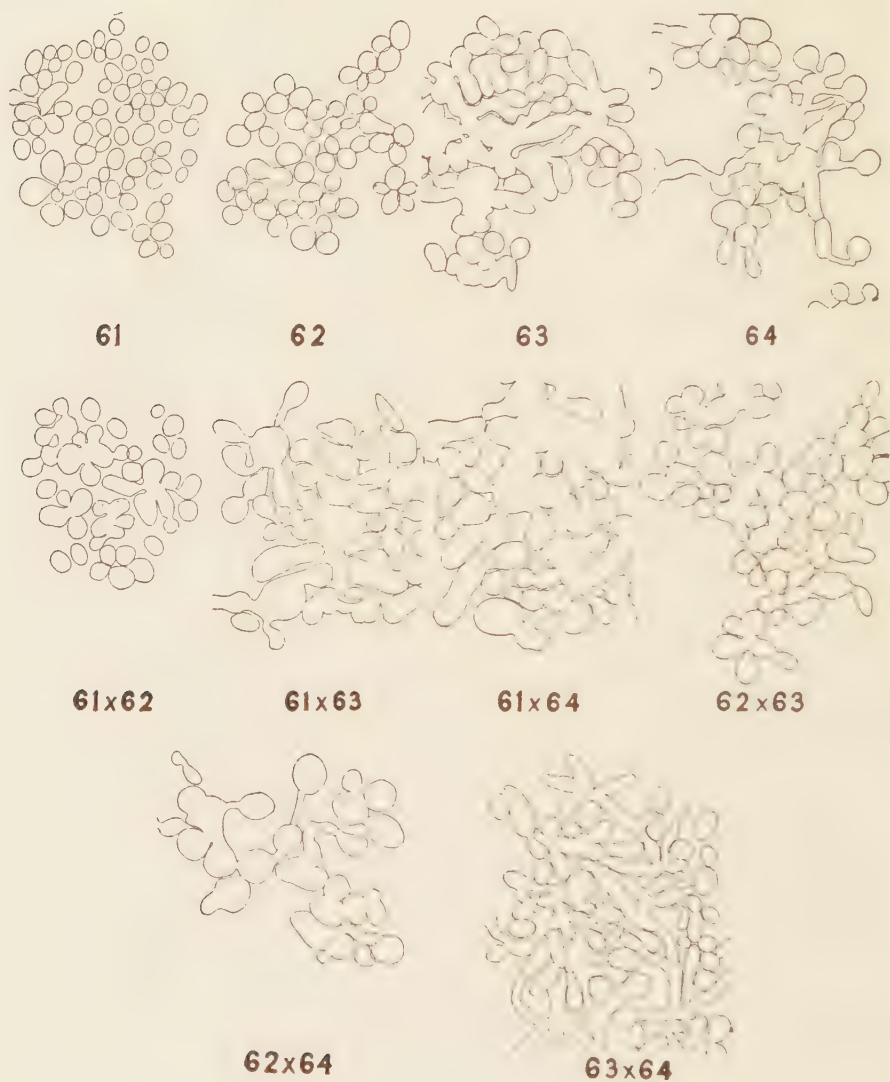


Fig. 2. Outline drawing of the cells of cultures 61, 62, 63, and 64, and all possible pairings from mating tubes in broth containing .5 per cent camphor.

number of 4-spored asci. The viability of the ascospores from cultures of this type is generally quite low, and the production of ascospores in culture 63 was also much lower than that of the four legitimate diploids.¹ Mating of 61 by 62 did not result in the production of ascospores, and fig. 1 shows that the mating had not resulted in cell fusion. The mating of 63 and 64 did not produce any more ascospores than 63 alone. Mating 62 by 64 resulted in the production of many asci only a few of which were 4-spored. The other three legitimate matings gave relatively high frequencies of 4-spored asci, with 62 by 63 conspicuously better than any of the others.

A duplicate experiment was carried out, using precisely the same methods except that 0.5 per cent camphor was added to the medium in which the matings were made. The outline drawings of the cells from the matings shown in fig. 2 indicate that cultures 61 and 62 were relatively insensitive to the effects of camphor, while in cultures 63 and 64 anastomoses occurred frequently. In the mating of 61 by 62, a few of the clusters are swollen, but the indications are generally consistent with the low sensitivity of these cultures to camphor. A mixture of 63 by 64 in the presence of camphor resulted in an excessive number of anastomoses. After growing these cultures on presporulation media, they were transferred to gypsum with practically the same results as obtained without the use of camphor. In the mating 62 by 64, 4-spored asci were very rare; the best 4-spored asci were produced by mating 62 by 63. The results of both matings were the same as in the absence of camphor. In spite of the abundance of anastomoses in the 63 by 64 mating, no more spores were produced by the combination than by 63 alone.

These results indicate that, except for structures similar to copulation tubes, matings in the presence of camphor were not able to effect combinations which did not occur in its absence. This does not prove that camphor is ineffective; it may be that, combined with other substances present in the type of beer wort used by Thaysen and Morris, copulations could be induced which would result in nuclear fusion. The importance of the subject warrants extensive examination of the phenomenon. Critical control experiments are required to exclude the alternative that the diploidization may have occurred spontaneously.

THE INSTABILITY OF THE MATING TYPES UNDER SELECTION PRESSURE

The transformation of the yeast cultures capable of copulation into neutral *Torulæ* explains the fact that many of the cultures from single ascospores which we carried in culture for a year or more were unable to copulate with freshly isolated tester strains capable of copulation. Apparently, the genes controlling copulation become unrecognizable by mutation under the selection pressure exerted on haploid cultures. These observations also explain the results

¹ The fields from culture 63, selected for the photographs, contained more than the average number of ascospores, but in photographing the other cultures, an attempt was made to select representative fields.

obtained by Winge and Laustsen ('37), who paired all the available *Torulæ* in all combinations and failed to obtain any diploid cells. When cultures are isolated in the haploid state, the survival value of the genes controlling copulation disappears and a new mutation, even if its advantage be very slight, would tend to replace either the *a* or the *a* genotype. It is not required that the new mutation appear at the *a* or *a* locus. It may be a modifier or *a* or *a* with some slight advantage over its parent type.

A second type of transformation with respect to copulation capability is found rather infrequently among single ascospore cultures. These variants produce an abundance of copulation tubes as soon as the culture reaches full growth. The cells from these cultures can copulate with the cells of any other culture capable of copulation and may produce diploid zygotes, irrespective of whether or not they are mated with either *a* or *a* mating types. The variants have lost the characteristic of discriminating between the *a* and *a* types. This non-discriminatory type may have been produced by a mechanism similar to that suggested by Sturtevant ('24) to explain orthogenesis. The gene producing copulation tubes may have either mutated to a gene which retains the quality of producing copulation tubes associated with another character of high survival value or may be closely linked to a second gene of high survival value. To quote Sturtevant: "If we suppose that the antlers of the Irish elk were dependent for their size upon testicular secretions, then selection may have increased the testicular secretions for reproductive or other reasons, and thus have resulted in a purely incidental increase in size of antlers." These haploid yeasts have been transformed into the "genus" generally recognized as *Zygosaccharomyces*.

The instability of genes controlling copulation in yeasts is paralleled by a similar instability at the *AB* loci in the *Hymenomycetes*. Two cultures of *Coprinus lagopus* collected from different dung heaps are completely interfertile (Hanna, '25) due to mutations at the *AB* loci. Vandendries ('37) extended this study to show that sterility factors can be demonstrated when *Hymenomycetes* from different continents are mated. The self-sterility alleles in *Neurospora* are extraordinarily stable (Lindegren, '32, '34), and of many single ascospore cultures examined we found no mutations at the *+/-* locus. Single ascospore cultures of *Neurospora* often lose their fertility when carried in culture; this is probably due to genes modifying the *+/-* factors. The fact that multiple mutants are less fertile than the wild type suggests that most mutant genes modify the *+/-* alleles to reduce fertility (Lindegren, Beanfield and Barber, 1939).

Haploid yeasts are astonishingly mutable. Subculturing a haplophase yeast produces a large variety of morphological mutants. If the *a/a* alleles are modified by these mutant genes, changes in fertility might occur. This would be especially true in a yeast culture, since the selection pressure is great and constantly varying, due to the effect of the growth of the organisms on the substrate. Diploid cultures are protected against variation by the presence of the normal allele at each locus to "cover" the mutant gene which is generally recessive. Homozygous

diploids are the most stable of all since they generally fail to produce viable haploid ascospores, and the diploid ascospores which they produce germinate to form clones indistinguishable from the parent type. A parallel stability with regard to mating type is found in completely homozygous diploid cultures of *Paramecium* (Sonneborn, personal communication) which are practically non-variable in their sex reactions.

Since haploid yeast cultures are sexually unstable, when subcultured vigorously the test for mating type can only be performed with single-ascospore cultures obtained from freshly isolated spores.

CRITERIA FOR DISTINGUISHING HAPLOID FROM DIPLOID CULTURES

Cell size alone is not a sufficient criterion for distinguishing diploids from haploids because cells in both types of cultures vary in size. Neither is cell shape in itself a satisfactory criterion of haploidy, for while the cells of haploid cultures are generally round many are distinctly ellipsoidal. Haploid cultures are usually more variable than diploid cultures, and old cultures may contain larger cells than do diploid ones. Comparative measurements of cell size must be made on young cultures grown under standard conditions in liquid medium. An example of the bloated, round cells frequently found in haploid cultures is seen in pl. 7c. Such cells invariably have an enlarged central vacuole, suggesting that increase in size is not due to any additional dry matter. Cells of this type, often much larger, are found in old cultures and can easily be distinguished from normal ellipsoidal, diploid cells. Extremely thin, elongated cells are also found in haploid cultures. Much of this variation is simply phenotypic, as is indicated by the fact that cells from different parts of the colony vary in size and shape (Lindegren and Hamilton, '44). Yeasts cultured on agar show a pseudomycelium of elongated cells growing into the substrate. The cells on the top of a colony of *Torula utilis* are often extremely elongated and much smaller than those found in liquid medium. Both bloated cells and long, thin cells are generally characteristic of haploid cultures, although many haploid cultures show a predominance of one or the other type. They are generally absent from diploid cultures.

Another fairly constant distinction between haploid and diploid cultures is that haploid cells often tend to form associations due to failure of the daughter cells to separate after budding. When only four cells are present in a cluster, the typical figure-8 configuration described by Winge ('35) results. These clusters may become rather large and are generally characteristic for specific mutant types. In forming clusters, the first bud does not always persist with its long axis perpendicular to the tangent of the cell surface. The persistent perpendicular bud is characteristic of diploid cultures.

A typical diploid cell produces only a single bud at a time. However, many haploid cultures contain single, large, round cells which produce many buds at the periphery. This type of budding has been used as a generic criterion in the

imperfect yeasts, but it is found not infrequently in single ascospore cultures isolated from the standard *Saccharomyces cerevisiae*.

Many haploid cultures contain pear-shaped cells resembling the first stage of copulation tube formation; in unmated haploid cultures, the stimulation required to complete the tube is not present. Pear-shaped cells are characteristic of apiculate yeasts.

Diploid cultures therefore differ characteristically from haploids in the following manner: (1) they generally fail to remain associated after the bud has attained full size; (2) only a single bud, generally at right angles to the cell surface, is formed; (3) they are generally more uniform in cell-size than haploid cultures; (4) there are practically no elongated, balloon or pear-shaped cells, while these forms abound in haploid cultures, especially in old ones.

In addition to a greater stability in cell-size and shape, diploid colonies are remarkable in producing uniform, large, smooth colonies, while haploid cultures produce a great variety of small, rough colonies (Lindegren and Lindgren, '43a).

CRITERIA FOR ESTABLISHING THE OCCURRENCE OF NUCLEAR FUSION IN YEASTS

When anastomoses are found in yeast culture, it is difficult to see whether or not true fusions have occurred. Cell fusions in the fungi are often without any sexual significance and are not necessarily followed by nuclear fusions. In different fungi, different criteria are relied upon to prove that copulation and nuclear fusion have occurred. In the *Hymenomycetes*, clamp connections are evidence of copulation but do not necessarily indicate that nuclear fusion will follow. In *Neurospora*, the development of perithecia and ascospores in mixed cultures proves that mixing the cultures has resulted in nuclear fusion. In the yeasts, copulation between the cells of mixed cultures followed by the production of the typical diploid cells is suggestive, but since copulation and diploid cells often occur spontaneously in haploid cultures diploid cells are not necessarily evidence that a hybrid has been formed. The occurrence of anastomoses in old haploid cultures at the center of the cell aggregations is in line with Winge's observations that the figure-8 conformation so frequently found in haploid yeasts is a preliminary to illegitimate copulation.

Nickerson and Thimann ('43) stated that when two cells of a *Zygosaccharomyces* are attached, budding can be distinguished from copulation by the fact that buds always occur with their long axis at right angles to the tangent of the cell surface. This is generally true of diploid cultures (see above) but they were working primarily with *Zygosaccharomyces*, which are haploid. In haploid cultures the clover-leaf cell aggregates are often formed by two secondary buds appearing near the point of attachment of the budded cells. There are indications of post-fission movement at the attachment point, which results in a change of the perpendicular attachment of the bud. The only conclusive proof that hybridization between the mixed cultures has occurred is the subsequent production of

large diploid cells capable of undergoing meiosis and producing viable 4-spored asci.

BIOLOGICAL IMPLICATIONS OF THE INSTABILITY OF THE MATING TYPE ALLELES

In nature a *Saccharomyces* which yields a large number of vigorous *Torulæ* will be at a disadvantage, for the *Torulæ* might displace the parent form. The *Torulæ* are a fundamentally less efficient biotype, since they are incapable of exploiting the sexual mechanism for effecting genic recombinations. In *Saccharomycodes*, all copulations occur in the ascus and no haplophase is found. Suppression of the haplophase in *Saccharomycodes* does not permit selective competition between gametes which occurs in *Saccharomyces* just previous to copulation. This competitive interphase eliminates the possibility of producing zygotes carrying lethal genes. In *Saccharomycodes*, where this competition is eliminated by direct fusion of ascospores, a balanced lethal mechanism associated with mating types develops as was found by Winge and Laustsen ('39) in *Saccharomycodes ludwigii*. In *Saccharomyces* the strength of the mating-type alleles is adjusted to permit the haploid spores to germinate and produce small colonies before copulation occurs. The greater vigor of the legitimate diploid enables it to swamp out the haploid cells, and relatively few *Torulæ* or *Zygosaccharomyces* are found in nature.

SUMMARY

Mating type alleles in *Saccharomyces cerevisiae* are unstable, and cultures capable of copulation become transformed in the laboratory into *Torulæ* incapable of mating with each other or with tester strains. The instability of the mating type alleles results in the selection of mutants of diminished fertility during the period that the isolated haplophase is grown in pure culture.

Structures resembling copulation tubes are produced by exposure of yeasts to camphor. We have not been able to induce nuclear fusions by mating cultures in the presence of camphor.

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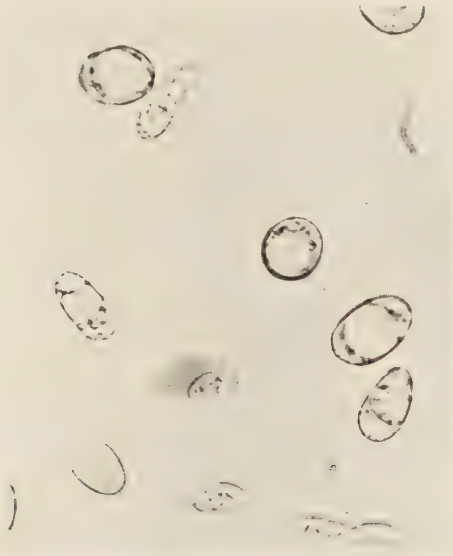
EXPLANATION OF PLATE

PLATE 7

Saccharomyces cerevisiae

The effect of camphor on diploid and haploid yeasts:

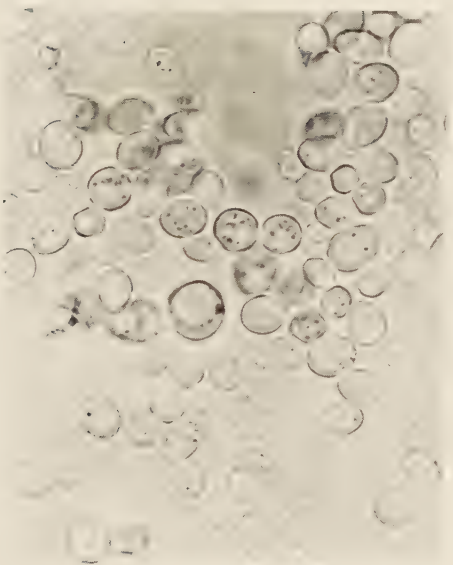
- a. Diploid culture of the Lk strain grown on a nutrient agar plate without camphor.
- b. Lk strain in same medium containing .3 per cent camphor.
- c. Haploid culture of M3 strain grown without camphor.
- d. M3 strain in medium containing .3 per cent camphor.



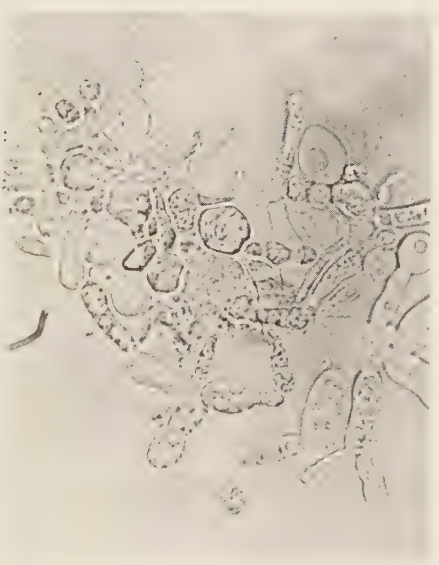
a



b



c



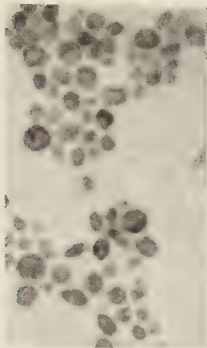
d

EXPLANATION OF PLATE

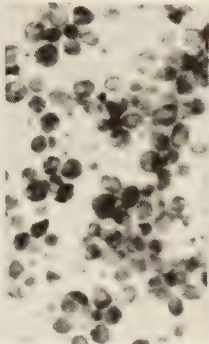
PLATE 8

Saccharomyces cerevisiae

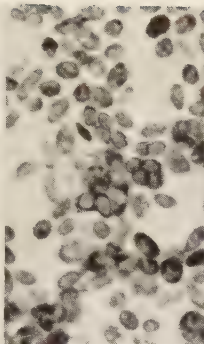
Cells from the gypsum slants originating from the cultures and pairings shown in text-fig. 1.



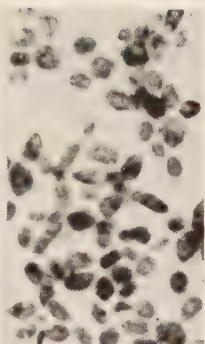
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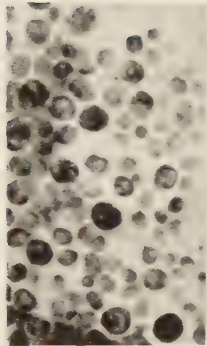
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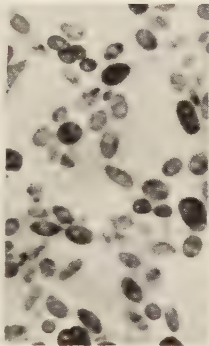
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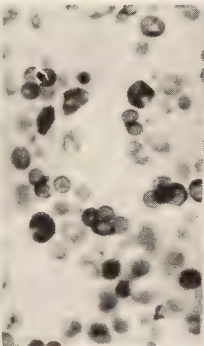
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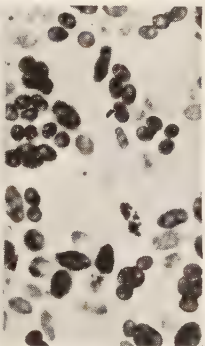
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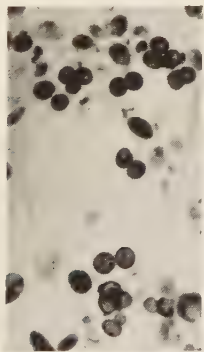
61 x 63



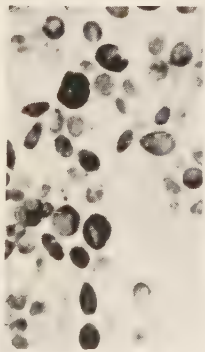
61 x 64



62 x 63



62 x 64



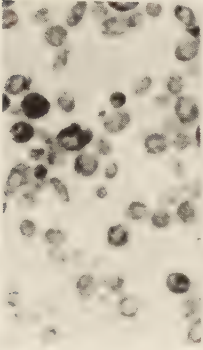
63 x 64

EXPLANATION OF PLATE

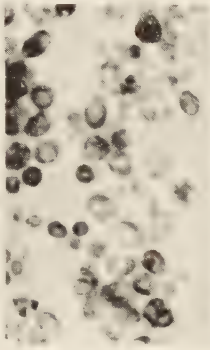
PLATE 9

Saccharomyces cerevisiae

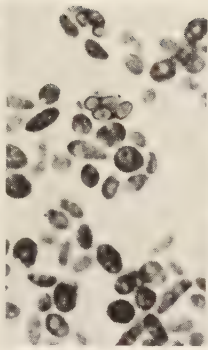
Cells from the gypsum slants originating from the cultures and pairings shown in text-fig. 2.



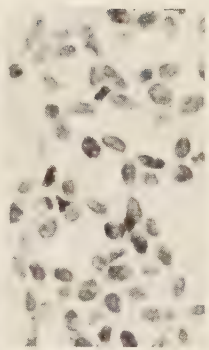
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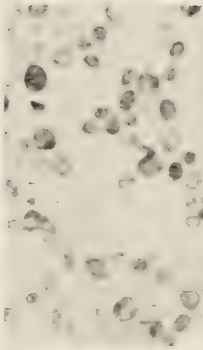
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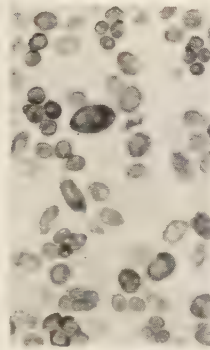
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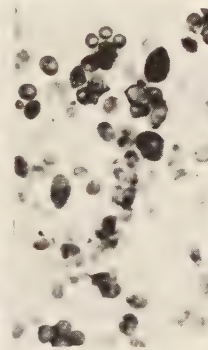
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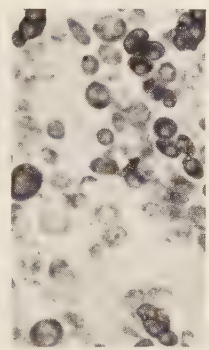
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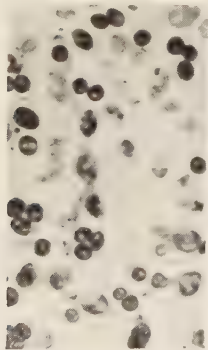
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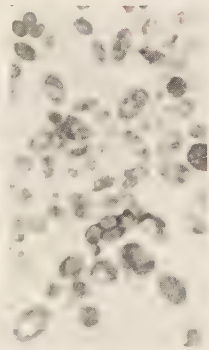
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A COMPARISON OF THE KINETICS OF ENZYMATIC ADAPTATION IN GENETICALLY HOMOGENEOUS AND HETEROGENEOUS POPULATIONS OF YEAST¹

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Populations of microorganisms possess the ability of undergoing striking changes in their physiological properties under the stimulation of substances in their environment. Such changes may involve either the acquisition of an enzyme system not previously detectable or the loss of one that it had possessed before the environmental change. An example of this phenomenon is the ability of certain yeasts to acquire the enzymatic apparatus necessary to ferment galactose. Since its discovery by Dienert ('00) this particular problem has been investigated by numerous workers. Armstrong ('05) confirmed Dienert's findings and further found that some yeasts were incapable of acquiring this physiological property no matter how long they were cultured in the presence of galactose. Slator ('08) showed that those yeasts capable of fermenting galactose possess this ability only after they had been acclimatized by culture in its presence. No yeast he investigated was able to ferment this hexose immediately upon being introduced to a medium containing it. There was always an induction period of variable length connected with the acquisition of this property.

Attempts to elucidate further the nature of this acclimatization or adaptation encountered a basic problem common to all studies of physiological changes in large populations. A comparative biochemical study of large populations always involves over-all populational characteristics. This necessarily introduces difficulties in the interpretations of any observed changes in physiological properties. The mechanisms available to an individual cell for adapting itself to an environmental change are limited by its genome and the physiological flexibility permitted by its particular degree of specialization. When, however, the adaptive ability of a population of cells is being considered, there must be added to the physiological pliability of its members the genetic plasticity of the group in terms of the numbers and kinds of variants it is capable of producing.

Because of this composite nature of populational adaptability, it is clear that in any particular case the same end result can be obtained by any one of the following mechanisms: (1) the natural selection of existent variants with the desired characteristics from a heterogeneous population; (2) induction of a new (as far as measurements of activity are concerned) enzyme by the substrate in all the members of a homogeneous population, resulting in an increase in the

¹ This work was aided in part by a grant from Anheuser-Busch, Inc., St. Louis.

measured enzymatic activity of the population; (3) a combination of natural selection and the action of mechanism (2) on those selected.

Several attempts have been made to decide which of the above mechanisms is involved in the adaptation to galactose fermentation. Sohngen and Coolhaas ('24) grew their yeast cultures at 30° C. and measured enzymatic activity at 38° C. to avoid cell division during the measurement of CO₂ evolution. They concluded from their experiments that the production of galactozymase parallels the formation of new cells. In addition, they confirmed Kluyver's ('14) findings that at 38° C., at which temperature cell division is completely inhibited, no adaptation takes place. Other investigators also tried to obtain adaptation in the absence of cell division since this would clearly exclude the operation of natural selection as a causal agent in effecting the change. Euler and Nilsson ('25), and later Euler and Jansson ('27) in a more thorough examination, tried adapting yeast to galactose fermentation in the presence of 0.5 per cent phenol to inhibit cell division. These attempts failed. They also repeated Kluyver's attempt to dissociate growth and adaptation by culturing the yeasts at 38° C., but again neither growth nor adaptation occurred. Stephenson and Gale ('37), using *Bact. Coli*, also concluded that adaptation to galactose in this organism was invariably accompanied by cell division. No evidence of adaptation was found in the absence of cell multiplication, and the increase in galactozymase activity in the growing population could be explained on the basis of the new cells formed.

The failure of the above-mentioned authors to find adaptation in the complete absence of cell division cannot be taken as conclusive evidence that no such phenomenon could exist. It is conceivable that in cultures where this "ideal" had been reached, the physiological state of the cells was such that their ability to synthesize new enzymes had been lost along with their ability to divide. Stephenson and Yudkin ('36) concluded from their experiments that the production of galactozymase in yeast cultures need not involve the formation of new cells. This conclusion was based on the observation that the ability to evolve CO₂ anaerobically from a medium containing galactose was acquired in a period when the total viable counts of the population remained constant. These adaptive periods were relatively long, extending to 24 hours, and the constancy of count was apparently obtained fortuitously in some of their experiments, though this was aided by using old cultures which had exhausted their polysaccharide reserves.

In view of the apparent contradiction between the findings of Stephenson and Yudkin and those of previous investigators (particularly Sohngen and Coolhaas) the present authors reinvestigated the problem from a different point of view (see Spiegelman, Lindgren and Hedgecock, '44, *hereafter referred to as* 1). They described a method (1) by which the phenotypic homogeneity of yeast populations could be examined with respect to the ability of the individual members to acquire the power to produce CO₂ rapidly from galactose. The method depends on the fact that a cell can generally be characterized by the type of colony it produces when grown on an agar surface under standard conditions.

Thus, if a representative sample of a population is plated out and more than one colonial type is noted, it may be concluded that more than one type of individual is represented in the population (see Shapiro, Spiegelman and Koster, '37). It will be noted that this method of plating out possesses the inherent advantage of providing in the process for the ecological isolation of the individual members of the sample population. This permits a relatively complete expression of any phenotypic heterogeneity which may exist but which might not otherwise be detectable due to the inhibitive competitive interaction amongst the phenotypes.

In order to distinguish between the rapid gas producers (fermenters) and those that could not ferment the sugar, advantage was taken of the fact that colonies which evolve CO_2 rapidly would, when growing between two layers of agar, produce typical star-shaped cracks in the agar of their immediate neighborhood. The quantitative validity and reproducibility of this detection method were examined and found to be satisfactory.

The reasons for developing this method are evident from the above discussion of the nature of populational adaptability, since one of the crucial points at issue in problems of this nature is the phenotypic homogeneity or heterogeneity of the starting population. Thus, if it can be shown that the initial population was phenotypically heterogeneous with respect to the ability of the individuals to demonstrate a property, then natural selection could operate to produce the change. If, on the other hand, the population can be shown to be homogeneous with respect to this property, any sudden change in the characteristic studied can more likely be ascribed to a direct cytoplasmic interaction with the substrate, the delay being due to an induction period.

Two strains of *Saccharomyces cerevisiae*, Db23B and LK2G12, both of which could acquire the ability to ferment galactose when grown in its presence, were examined by this method. Strain Db23B, which was known to be haploid and therefore genetically unstable (see Lindegren and Lindegren, '43 a, b, c, d, for further details concerning yeast breeding and strain isolation), was shown to be phenotypically heterogeneous with respect to galactose fermentation. It contained two types as far as behavior towards galactose was concerned: One could not adapt to galactose fermentation while the other one could. Strain LK2G12, on the other hand, which was known to be diploid, was uniformly homogeneous in that all of its individuals were able to acquire the capacity for fermentative utilization of galactose on standing in contact with the sugar. The pre-adaptive period of this strain under the conditions of the experiments was three hours, which is characteristic for this particular strain under standard conditions, and has been duplicated many times over a 7-month period. This is apparently much shorter than the periods encountered by Stephenson and Yudkin. Because of the relative rapidity of adaptation of this strain, experiments may be performed on the mechanisms of the process that can rule out cell divisions without drastic inhibitory treatments which might interfere with other physiological functions.

The adaptive behavior of these two strains followed what would be expected from the data obtained on their phenotypic characteristics. Populations of Db23B, starting with a low percentage of the fermenting type, could increase their enzymatic activity only through the mechanism of cell division and the subsequent selection in favor of galactose fermenters. In no case was increased enzymatic activity observed without parallel increase in cell numbers. However, this was not true of LK2G12, in which adaptation could occur without any measurable change in total cell number. From the results with these two strains the existence of both the "natural selection mechanism," as well as that of direct cytoplasmic interaction, was concluded. Which one was operative depended upon the genetic stability and composition of the population.

It will be noted that the conclusion that natural selection operated in changing the characteristics of Db23B populations depended on two types of evidence, namely: the phenotypic heterogeneity of the initial populations with respect to galactose fermentation; and the inability of this strain to increase its enzymatic activity in the absence of cell division when placed in contact with galactose.

As pointed out previously, the absence of increasing enzyme activity in a non-dividing culture has little crucial interpretive value. It does, however, become more meaningful when combined with evidence of phenotypic heterogeneity. Nevertheless, it would clearly be desirable to demonstrate the operation of natural selection more positively by showing its existence in growing populations of Db23B rather than inferring its existence by the absence of adaptation when it is not operating. It is the particular purpose of the present paper to offer such data on growing cultures of Db23B. A theory capable of handling the quantitative analysis of its significance will also be presented. For purposes of comparison similar data will also be presented on two diploid strains, LK2G12 and 812, both of which can adapt without cell division. It will be shown that the time-variation of the ratio of the two phenotypes in a Db23B population growing on galactose is quantitatively described by a "natural selection" mechanism. It will furthermore be shown that the dependence of enzymatic activity on increasing cell numbers in growing populations of Db23B also leads to the conclusion that natural selection is involved.

MATERIALS AND METHODS

A. Yeast strains.—Three strains of *Saccharomyces cerevisiae* isolated in this laboratory and known as Db23B, LK2G12 and 812 were used in the following experiments. Strain Db23B originated from a single ascospore, and since its population contains principally haploid cells it is characteristically unstable. Strain LK2G12 originated from an intact 4-spored ascus in which copulation was observed to occur pairwise. Consequently it is known to be a diploid and in contrast to the Db23B is characteristically stable. Strain 812 is known to be diploid on similar grounds.

B. Media.—The basic medium was made as follows: Into 1 liter of fluid was

dissolved 5 gms. peptone, 1 gm. MgSO_4 , 2 gms. KH_2PO_4 , 4 cc. of 80 per cent sodium lactate, 2 cc. liquid yeast extract, and to this was added the carbohydrate in an amount sufficient to make an 8 per cent solution. Agar plates were made by adding the requisite amount of agar to the above basic medium. The broth medium was always cleared by filtration before distribution to separate flasks for autoclaving. This clearing process was essential in the agar medium to facilitate observation of the colonies on test plates.

C. *Carbohydrates*.—Reagent grade glucose was used. The galactose was Difco's purified further treated according to a method described by Stephenson and Yudkin ('36) to remove any contaminating fermentable sugars.

D. *Test plates*.—These are double-layered agar plates containing 4 per cent galactose purified as described above. Colonies grew between the layers and those that could ferment galactose evolved gas at a sufficient rate to produce the typical star-shaped cracks in the agar in their immediate neighborhood. To test the type composition of a sample population the following procedure was used: The sample was centrifuged down and washed free of any glucose with $\text{M}/15 \text{ KH}_2\text{PO}_4$, if it came from a glucose medium. The washed cells were then resuspended in chilled galactose broth and diluted to contain approximately 5,000 cells per cc. Of this suspension approximately 0.1 cc. was then placed on a 4 per cent galactose-4 per cent agar surface from which all excess fluid had been allowed to drain. Even distribution was obtained by rotating a sterile bent rod over the surface. A 5 per cent agar medium containing 4 per cent galactose, cooled to 39°C. , was poured over the inoculated surface. These test plates were incubated at 28°C. for at least 48 hours before a count was taken. Usually five test plates were prepared from each suspension it was desired to examine, and the results averaged. Counting was done under the low power of a dissecting microscope.

E. *Manometric measurements*.—Warburg vessels, capable of being flushed with gas, were used. All measurements were taken at 30.2°C. , the vessels being shaken at a rate of 100 oscillations per minute. The nitrogen used to displace the air in measurements of anaerobic CO_2 production was passed over hot copper to remove any traces of oxygen.

F. *Cell counts*.—Cell counts were made by means of a Spencer bright-line haemocytometer.

THE "NATURAL SELECTION" HYPOTHESIS

One type of data that is relatively easy to obtain by the use of the galactose test plates is the time-variation of the ratio of fermenters to non-fermenters in a population growing on a galactose medium. It should be possible to use these data to test whether the kinetics of the shift of this ratio in favor of the fermenting type in a growing culture fits that which would be predicted on the basis of a natural selection mechanism. To make such an examination it is necessary to find the functional dependence between the ratio of the two types and time, deducible from a simple selection theory. It would be desirable to transform this

into a linear relation for convenience in testing the goodness of fit.

A functional relation of this type may be found by a simple mathematical description of a selection theory. In the previous paper (1) it was shown that both phenotypes were always present even in glucose-grown cultures. It may be assumed that the fermenters arose through variations from the non-fermenters due to the genetic instability of the haploid populations. This genetic instability is also shown through the numerous morphological variants which such cultures invariably exhibit on plating (Lindegren and Lindgren, '43a).

From the point of view of natural selection the course of the phenomenon subsequent to transferring a glucose-grown Db23B population to a medium containing galactose as the sole source of carbohydrate may be described as follows: The non-fermenters can only use galactose slowly through a purely aerobic type of oxidation¹ and therefore their rate of division is depressed in this medium. The few fermenters present, after a lag period, start to divide rapidly since they possess the enzymatic apparatus necessary to use this sugar at a rapid rate. The number of fermenters thus increases due to two sources: first, the rapid cell division of those already present, and second, the mutation of the non-fermenting type to the fermenting kind. This latter mechanism can, even with relatively low mutation rates, be numerically significant in the early history of the populations because of the relatively large number of non-fermenters initially present. On the other hand, the number of non-fermenters present at any time can increase only by virtue of the cell divisions of this type.

If we let U represent the number of non-fermenters (unadapted cells) at any time (t), and A the number of fermenters (adapted cells) the above discussion leads to the following two differential equations

$$(1) \quad \frac{dU}{dt} = cU$$

$$(2) \quad \frac{dA}{dt} = aA + bU$$

In these equations c is the growth constant or "biotic potential" of U in a galactose medium and a has a similar significance for the adapted phenotype. The constant b measures the relative rate at which the A -type is thrown off during the cell divisions of the U -type. Equations (1) and (2) describe the growth rate of the two phenotypes in a heterogeneous population. Equation (1) may be solved directly to yield U as the following function of time,

$$(3) \quad U = U_0 e^{ct}$$

where U_0 is the number of unadapted cells present at zero time. From equation (3) it is seen that

$$c = \frac{1}{t} \ln \frac{U}{U_0}$$

¹ This purely aerobic utilization of galactose by unadapted cells will be described in detail and discussed in a later publication.

and consequently the constant may be obtained as the slope of the line obtained by plotting $\ln \frac{U}{U_0}$ against time. With the aid of equation (3), equation (2) may be solved to yield

$$(4) \quad A = (A_0 - \frac{b U_0}{c-a})e^{at} + \frac{b}{c-a} U_0 e^{at}$$

where A_0 is the number of adapted cells present at t equal zero. The magnitude of the constant a may be obtained from the growth rates of a fully adapted culture when growing on galactose, since under those conditions,

$$\frac{dA}{dt} = aA$$

Equations (3) and (4) express the absolute numbers of both phenotypes as functions of time. Absolute numbers are difficult to obtain with any precision. Furthermore, the use of these equations as they stand to test the theory would involve the relatively accurate determinations of the constants a , b and c . A simpler way of testing the theory exists in terms of ratios of phenotypes. It will be remembered that the test plates yield data on the ratio of A to U , and this $\frac{A}{U}$ may be obtained directly from equations (3) and (4). To facilitate computations, equation (4) may be simplified without destroying its usefulness in testing the validity of the selection theory. By using the methods described above, the constant a was found to have a value of 2.1, whereas c under the same conditions was only 0.1. The constant c may therefore be neglected in comparison with a in equation (4) since they both appear always additively. On the same numerical basis A_0 may also be ignored.

These simplifications are ones that do not involve the linearity of the final relation to be tested while contributing to the ease of the mathematical manipulation. Equation (4) thus becomes

$$(5) \quad A = \frac{b}{a} U_0 e^{at} - \frac{b}{a} U_0 e^{at}$$

Dividing the equation (5) by (3) and again neglecting c in comparison with a , we find

$$(6) \quad \frac{A}{U} = \frac{b}{a} (e^{at} - 1)$$

Equation (6) may be put into a more convenient linear form by dividing by $\frac{b}{a}$, transposing and taking logarithms of both sides. We thus obtain

$$(7) \quad at = \ln \left[\left(\frac{a}{b} \right) \frac{A}{U} + 1 \right]$$

The theory then predicts a linear relation between time and the function of $\frac{A}{U}$

represented on the right-hand side of equation (7). It must be pointed out that the linearity of this relation is independent of the accuracy of the values obtained for the constants a and b since they remain the same throughout the experiment. In point of fact, as far as testing the theory is concerned, any arbitrary number may be substituted for the ratio $\frac{a}{b}$. The only requirements imposed on these numbers is that a be assumed finite and b taken as greater than zero. For purposes of calculations a value of 200 was taken for b , since several estimates of b gave values lying between 0.005 to .01.

EXPERIMENTAL RESULTS

The following typical experiment was performed to test the validity of relation (7) in describing the time-variation of $\frac{A}{U}$ for a Db23B culture growing on a galactose medium. A two-day-old culture growing in the normal glucose broth medium was centrifuged down and washed twice with M/15 KH_2PO_4 under sterile conditions. The washed cells were then inoculated into the basic broth medium containing 8 per cent purified galactose as the sole carbohydrate source. The flask containing the culture was then suspended in a water bath at 30.2°C . and shaken continuously during the experiment. Samples were withdrawn at intervals and diluted with chilled galactose broth to contain approximately 5,000 cells per cc. This diluted suspension was used to prepare 5 galactose-agar test plates, approximately 0.1 cc. being used for each plate. After a suitable incubation period the ratio $\frac{A}{U}$ was determined from these test plates and the average value taken. The results are tabulated in table I in which are also calculated the values of the function of $\frac{A}{U}$ to be tested. Figure 1 represents the plot of $\log \left[\left(\frac{a}{b} \right) \frac{A}{U} + 1 \right]$ against time. It is clear from the figure that the data do satisfy the linear relation required by the natural selection hypothesis.

TABLE I

DATA EXAMINING THE VARIATION OF A/U WITH TIME IN A GROWING HAPLOID POPULATION TO SEE WHETHER IT SATISFIES THE RELATION PREDICTED BY THE SELECTION THEORY

(A represents the number of fermenters present, U the number of non-fermenters. The ratio a/b is taken as 200.)

| Strain | Hours | A/U | $\log \left[\left(\frac{a}{b} \right) \frac{A}{U} + 1 \right]$ |
|--------|-------|--------|--|
| Db23B | 2 | 0.11 | 1.301 |
| | 4 | 0.20 | 1.613 |
| | 12 | 0.49 | 1.920 |
| | 24 | 4.20 | 2.700 |
| | 32 | 5.00 | 3.080 |
| | 48 | 166.00 | 4.211 |

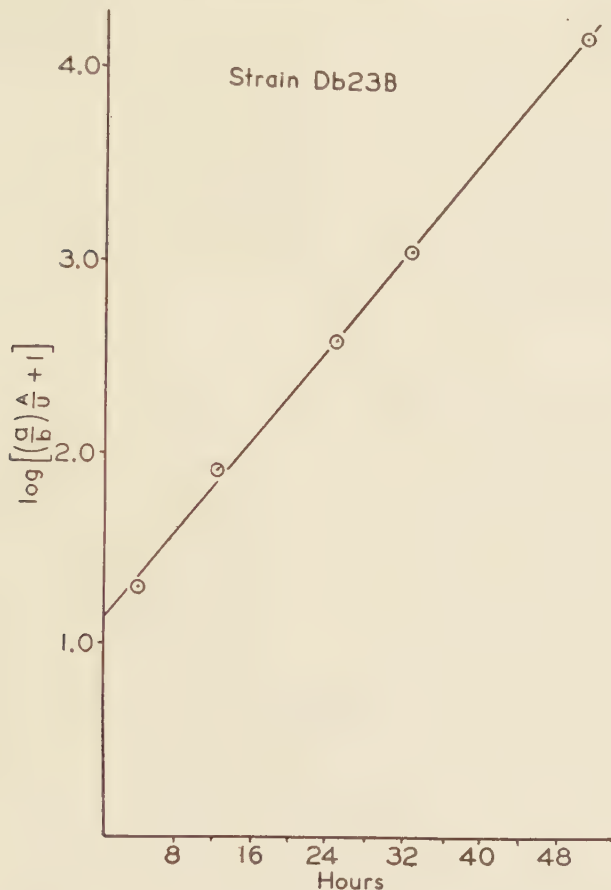


Fig. 1. A plot of data from table 1 to see how closely the time variation of phenotype ratios, obtained with a growing haploid population, satisfies the linear relation predicted by the selection theory.

For comparative purposes an attempt was made to see how well data obtained with strain LK2G12 would fit the theoretical relation deduced from the selection theory. The test plates could not, however, be used to obtain the necessary data, since they measure the ability of acquiring the fermentative enzymatic apparatus, and it has already been shown (see (1)) that populations of this strain are homogeneously positive. The reason for this, of course, exists in the fact that the incubation time (36–48 hours) necessary before the plates can be read by far exceeds the pre-adaptive lag period of the cells of this strain. The following method was used, however, to obtain comparable data. The maximum enzyme activity for this strain under the conditions of the experiment was measured and found to be 165. This number represents the $Q_{CO_2}^N$ value, i. e., cu. mm. of CO_2

liberated per hour per mg. of dry weight of tissue at normal temperature and pressure. This maximal value of 165 is presumably obtained when all the cells of the population are adapted. If the enzymatic activity of a suspension is less than maximal, it may be assumed, for the purposes of the present discussion, to be due to the fact that unadapted cells form some fraction of the population being tested. Under these conditions we may then take the $Q_{CO_2}^N$ value measured at any time t as proportional to A , the number of adapted cells present, whereas the difference $(165 - Q_{CO_2}^N)$ may be assumed proportional to U , the number of unadapted present. Following this reasoning then we may write

$$\frac{A}{U} = \frac{Q_{CO_2}^N}{(165 - Q_{CO_2}^N)}$$

To obtain the necessary data the following experiment was performed: a two-day glucose-grown culture of LK2G12 was centrifuged and washed twice in $M/15 \text{ KH}_2\text{PO}_4$ under sterile conditions. The washed cells were inoculated into basic broth medium containing 8 per cent galactose as the sole source of carbohydrate. The flask containing the culture was shaken continuously during the experiment in a bath at 30.2°C . Samples were removed at intervals and placed in Warburg manometers to determine the rate of CO_2 evolution in an atmosphere of nitrogen. A 20-minute run after equilibration was sufficient to determine the $Q_{CO_2}^N$ value. Aliquots were taken at the same time for dry-weight determinations. The results of such an experiment, as well as the calculations of the requisite functions from the data, are summarized in table II.

TABLE II

DATA EXAMINING THE VARIATION OF A/U WITH TIME IN A DIPLOID POPULATION(Consult text for method of calculation of A/U .)

| Strain | Hours | $Q_{CO_2}^N$ | A/U | $\log \left[\left(\frac{A}{U} \right) \frac{A}{U} + 1 \right]$ |
|--------|-------|--------------|-------|--|
| LK2G12 | 1.0 | 0.01 | 0.00 | 0.000 |
| | 2.0 | 0.03 | 0.00 | 0.000 |
| | 2.8 | 2.10 | 0.01 | 0.401 |
| | 3.3 | 45.00 | 0.30 | 1.803 |

Figure 2 represents a plot of these data similar to the one made for the data obtained with strain Db23B. The theoretical curve, based on the Db23B data, is plotted on the same graph for purposes of comparison since the time scales in the two experiments were necessarily different. It is evident that the kinetics of the appearance of enzymatic activity in a LK2G12 population does not fit a natural selection mechanism.

One other kind of experiment can be performed on a growing culture to check the applicability of the natural selection hypothesis, viz. the type performed by Solhngen and Coolhaas ('24). If this mechanism is operating in producing the change in the enzymatic level, the activity of a culture measured during the

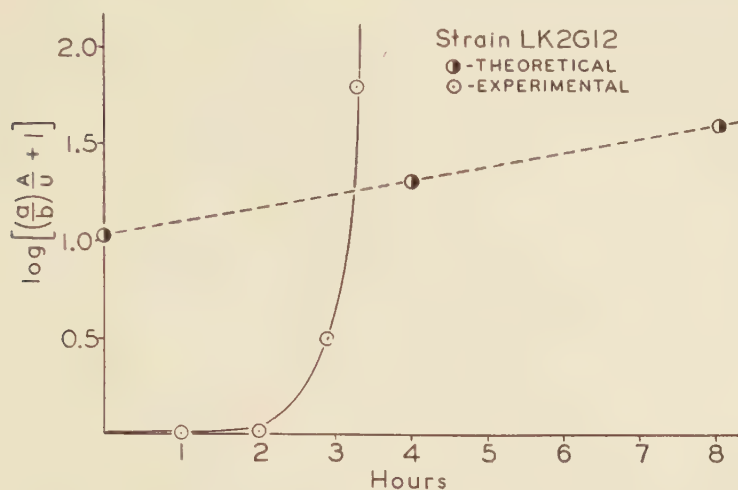


Fig. 2. A plot of data from table II to see how well data on the time variation of phenotype ratios, obtained from a diploid culture, agrees with the linear relation predicted by the selection theory.

growth phase should increase in direct proportion to the number of new cells arising during the period of growth. Thus a plot of enzyme activity against cell number should yield a straight line. It is, however, not necessary to grow the culture at one temperature and test enzyme activity at another as was done by Sohngen and Coolhaas. The Warburg manometric technique is sufficiently sensitive to yield $Q_{CO_2}^N$ of adequate accuracy by a 15–20-minute run. This period is too short for any marked change to occur in cell count, especially since the cells are under anaerobic conditions. This technique was apparently not available to the above workers, for they used a much cruder aerobic technique.

The following experiment was performed to test whether the increase in enzyme activity observed with growing cultures of Db23B could be accounted for on the basis of the new cells arising during the experimental period. A 2-day glucose-grown culture of Db23B was centrifuged down and washed once in M/15 KH_2PO_4 . The washed cells were then resuspended in the basic broth containing 8 per cent of purified galactose as the sole carbohydrate source. The density of the initial suspension was adjusted to contain 15 cells per 16 small squares. This corresponds to 40,000 cells/mm³. In practice, the cells were counted in the large squares, each of which was composed of 16 small squares. The data were recorded in terms of number of cells per large square.

The flask was shaken in a bath at 30.2° C. during the experiment. Samples were withdrawn at intervals for cell counts, and measurements were taken of enzyme activity in terms of cu. mm. of CO_2 liberated per 10-minute period per 2 cc. of suspension under anaerobic conditions. Cell counts were always made at the beginning and end of the manometric determinations and in all cases remained the same within the limits of the measurement.

The data obtained with Db23B are summarized in table III. Each value for the rate of CO_2 evolution represents the average over three 10-minute periods or four 5-minute periods. The latter was used in the last three measurements because of increased activity. Each figure in the column giving the number of cells per large square represents the average value obtained by counting 10 such squares in each sample.

TABLE III

EXAMINATION OF DEPENDENCE OF GALACTOZYMASE ACTIVITY ON INCREASE IN CELL NUMBER IN HAPLOID (Db23B) AND DIPLOID (812) POPULATIONS

| Strain | Hours | No. of cells per square | mm. ³
CO ₂ evolved per
10 min./2 cc. |
|--------|-------|-------------------------|--|
| Db23B | 0 | 15.7 | 0.03 |
| | 3 | 18.1 | 17.1 |
| | 4 | 21.0 | 16.0 |
| | 5 | 23.8 | 29.1 |
| | 6 | 26.3 | 34.0 |
| | 7 | 28.8 | 47.2 |
| | 8 | 30.1 | 50.2 |
| 812 | 0 | 16.6 | 0.2 |
| | 1 | 15.8 | 4.0 |
| | 2 | 17.0 | 23.5 |
| | 3 | 16.9 | 50.0 |
| | 3.5 | 17.3 | 70.0 |

At the same time, for purposes of comparison, a similar experiment was performed with strain 812, which has an adaptation period of two hours and is phenotypically homogeneous. In the case of 812, however, the washed cells were resuspended in $\text{M}/15 \text{ KH}_2\text{PO}_4$ containing 8 per cent galactose rather than broth.

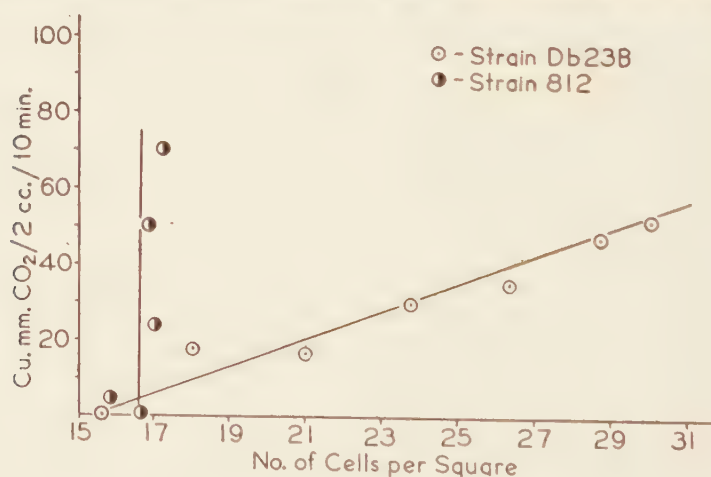


Fig. 3. A comparison of the dependence of galactozymase activity on increase in cell numbers in a haploid (Db23B) and a diploid (812) yeast strain.

This was done to minimize cell division in this experiment and thus accentuate the difference in the mechanisms used by these two strains to attain the change in galactozymase activity. All other experimental conditions were exactly as those imposed in the experiments with Db23B. The data for strain 812 are also recorded in table III. Figure 3 illustrates the type of dependence obtained between cell numbers and increase in enzyme activity. It is strikingly apparent that populations of the haploid strain, Db23B, increase their enzyme activity by virtue of the new cells arising during the experimental period. On the other hand, the measured activity of the 812 population was, in the period examined, virtually independent of cell number. This strain was able to increase its activity from zero to an activity level of 70 while maintaining its population at the same density.

DISCUSSION

The examinations of the variation of the two phenotypes with time in growing cultures of the haploid strain, as well as the dependence of enzyme activity on increases in cell number, lead to the conclusion that the appearance and increase of galactozymase activity in cultures of Db23B involve natural selection. Comparison with similar data obtained with the two diploid strains, both of which can adapt without cell division, further strengthens this conclusion. The data presented here on growing populations agree with the results obtained (1) on stationary cultures of the haploid strain.

From these results it is clear that the contradiction noted between the results of Stephenson and Yudkin ('36) and those of earlier workers is only an apparent one and is probably due to the differences in the genetic background and phenotypic constitution of the strains employed.

More generally, the conclusion may be drawn that it is impossible to decide, as some previous authors have tried to do, between the "natural selection" hypothesis and one of "direct cytoplasmic interaction" as the explanation for the production of a particular adaptive enzyme. The existence of one mechanism does not necessarily exclude the other from effecting the production of the same enzyme, as is well illustrated by the nature of the adaptation of galactose fermentation by the haploid and two diploid strains examined.

These experiments then emphasize the important point that the particular biological mechanism involved in the production of a given enzyme or enzyme system in a population of cells is a characteristic of the strain being examined rather than of the enzyme system itself. It is thus meaningless to ask and impossible to answer the question of mechanisms of enzymatic adaptation without referring to the genetic background and stability of the population studied.

The results with Db23B further emphasize the necessity of eliminating natural selection in any experiments the purpose of which is the detailed investigation of the biochemistry of the adaptive process itself. In this strain the rate of increase in measurable enzymatic activity depends not only on the synthesis of the requisite enzymatic systems but also on the rate of cell division. Any procedure which

interferes with the physiology of the latter process necessarily will affect the amount of enzyme measured. For investigations into enzyme synthesis strains should be used which possess (1) a genome which permits the synthesis of the enzyme being studied, and (2) the genetic stability to insure reproducibility of the physiological characteristics of the populations.

The two diploid strains, 812 and LK2G12, both satisfy these requirements and have been used to examine the conditions leading to the synthesis of the galactozymase system and the nature of the preadaptive period. These results will be discussed elsewhere.

SUMMARY AND CONCLUSIONS

(1). Data are presented on the kinetics of the replacement of a phenotype incapable of fermenting galactose by one that can acquire the property in genetically unstable haploid populations growing on galactose broth. The nature of the time-variation of the ratio of the two types is shown to fit a relation deduced from a selection theory.

(2). This was compared with comparable data on a diploid strain which did not obey the predicted relation.

(3). The kinetics of the increase in enzyme activity of the haploid populations was studied and shown to depend on the number of new cells which arose. A similar study on a diploid strain showed that increase in enzyme activity could take place in the absence of cell division.

(4). The general significance of these results for the problems of enzymatic synthesis and the induction of new physiological properties in populations of cells is discussed.

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MISCELLANEOUS NEW ASCLEPIADACEAE FROM TROPICAL AMERICA

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CYNANCHUM (METALEPIS) Marsdenioides Woodson, spec. nov. Frutex volubilis lactescens usque 5 m. vel ultra attingens; ramulis crassiusculis juventate minute puberulis mox glabratis post exsiccationem conspicue striatis pallidis. Folia opposita longe petiolata late ovato-elliptica basi late cordata apice abrupte longiuscule acute acuminata 14–16 cm. longa 9–10 cm. lata firme membranacea glabra nervo medio supra basi conspicue pectinatim pluriglanduloso, petiolis 7–8 cm. longis. Inflorescentiae (ramuli florigerentes aphylli) axillares oppositae, pedunculo 15–26 cm. longo crassiusculo minute puberulo-striato, internodiis basi 6–8 cm. longis apicem versus gradatim brevioribus, ramulis bostrycino-racemosis plurifloris unilateraliter 2–3-natim positis inaequilongis 2–6 cm. longis aliquando more pedunculi primarii compositis, pedicellis 0.4 cm. longis minute puberulis. Calycis lobi oblongo-lanceolati ca. 0.35 cm. longi glabri. Corolla ut videtur gilva vel viridula rotata, lobis ovatis acuminatis ca. 0.2 cm. longis 0.15 cm. latis basi concavis extus glabris intus apicem versus pilosis. Corona plane cyathiformis ca. 0.2 cm. diam., lobis 5 quadratis intus minutissime papillatis marginibus anguste involutis. Gynostegium breviter (ca. 0.05 cm.) stipitatum disciforme ca. 0.2 cm. diam., stigmatibus umbonatis; pollinibus pendulis anguste reniformibus ca. 0.05 cm. longis, caudiculis subhorizontalibus ca. 0.1 cm. longis, corpusculo mediocri. Folliculi ut dicitur fusiformi 22–25 cm. longi ca. 10 cm. crassi.—ECUADOR: LOS RIOS: Oct., 1934, Y. Mexia 6660, whence grown from seed at Puerto Rico Experiment Sta. U. S. D. A., Mayaguez, P. R., R. H. Moore 2163 (U. S. Nat. Arb. Herb., TYPE).

Most closely related to *C. Haughtii*, also of Ecuador, but with very precise distinctions: *C. Haughtii* has more deeply concave corolla-lobes; the corona segments are sharply inflexed, are conduplicate-emarginate, and are separated by smaller, alternate lobules; the sepals are proportionately broader and pilosulose

(235)

without; the caudicles of the pollinia are somewhat shorter and are concealed by the anther appendages whilst they are conspicuous in *C. Marsdenioides* as in *C. cubense*.

It may be worth while at this juncture to comment upon the compound "inflorescence" of the various species of *Cynanchum* subgen. *Metalepis* which differ superficially from the inflorescence of most other Asclepiadaceae in their truly axillary position. As is well known, the true inflorescence of Asclepiadaceae generally is extra-axillary and interpetiolar. An examination of any of the five published species of *Cynanchum* subgen. *Metalepis* demonstrates that the inflorescences, all compound and axillary, are homologous with the vegetative branches, since the flowering secondary peduncles are borne in an extra-axillary or "interpetiolar" position with respect to the bracts (*i. e.* reduced foliage leaves).

CYNANCHUM (METALEPIS) peraffine Woodson, spec. nov. Frutex volubilis lacteus; ramulis gracillimis glabris, internodiis elongatis. Folia opposita late ovata apice abrupte subcaudato-acuminata basi rotundate cordata 5-9 cm. longa 3-6 cm. lata tenuiter membranacea utrinque glabra nervo medio supra basi glanduligera; petiolis tenuibus 2.5-4.0 cm. longis glabris. Inflorescentia axillaris longiuscule pedunculata congeste bostrycino-racemosa pluriflora, pedunculo 2.5-4.0 cm. longo apicem versus florigero ibique puberulo basim glabro, pedicellis 0.2-0.3 cm. longis puberulis. Calycis lobi ovato-lanceolati acuminati extus minutissime sparseque pilosuli. Corolla alba, tubo cylindrico ca. 0.15 cm. longo ca. 0.2 cm. diam. extus glabro, lobis ovato-lanceolatis acutis 0.5 cm. longis patulis margine revolutis extus glabris intus margine dense puberulo-papillatis. Corona cyathiformis, lobis 5 acute emarginatis ca. 0.05 cm. longis minute papillatis compositis. Gynostegii stipes conicus ca. 0.08 cm. altus dense papillatus; stigmatibus umbonatis cum antheris ca. 0.3 cm. diam.; pollinibus pendulis anguste reniformibus ca. 0.08 cm. longis, caudiculis ca. 0.1 cm. longis, corpusculo mediocri. Fructus ignoti.—**MEXICO: OAXACA:** in llanos, Distr. Tuxtepec, Chiltepec and vicinity, alt. about 20 m., July, 1940-Feb., 1941, *G. Martínez-Calderón 258* (U. S. Nat. Herb., no. 1,808,120, TYPE).

Very closely related to *C. cubense* (Griseb.) Woods., which has mucronate or more gradually acute leaves, apparently of heavier texture, and somewhat smaller flowers with campanulate corolla tubes and nearly quadrate corona lobes. The two species present an interesting case of geographic parallelism.

MATELEA (EUMATELEA § RETICULATAE) serpens Woodson, spec. nov. Fruticulus volubilis prostratus; ramulis tenuibus longiuscule pilosis, internodiis sat elongatis. Folia opposita ovato-lanceolata apice longe acuminata basi late cordata 3-5 cm. longa 1.5-2.5 cm. lata membranacea utrinque plus minusve pilosa nervo medio supra basi inconspicue glanduligera, petiolis tenuibus 1.5-2.0 cm. longis longiuscule pilosis. Inflorescentia extra-axillaris longe pedunculata umbelliformis pluriflora, pedunculo 2-4 cm. longo tenui laxo piloso, pedicellis tenuibus in flore ca. 1 cm. longis post anthesem conspicue elongatis, bracteis conspicuis foliaceis linearibus longe acuminatis 0.4-0.8 cm. longis. Calycis lobi ovato- vel oblongo-

elliptici acuti in flore 0.6 cm. longi post anthesem ad 1 cm. accrescentes conspicue foliacei extus longiuscule pilosi glandulis minutis sessilibus brunneis interspersis. Corolla rotata ca. 1.3 cm. diam. ut videtur gilva; lobis ovato-ellipticis acutis ca. 0.5 cm. longis extus medio pilosis intus glabris. Corona vix manifesta, limbus inconspicuissimus gynostegio basi solum annectus. Gynostegii stipes ca. 0.1 cm. longus 0.15 cm. crassus; stigmatate late conico ca. 0.2 cm. diam. 0.1 cm. alto luteo; antheris sub stigmatate positis; polliniis horizontalibus obpyriformi-subcoclearibus profunde excavatis cum caudiculis alatis ca. 0.08 cm. longis, corpusculo minuto. Folliculi ignoti.—MEXICO: NUEVO LEON: on Pan American Highway, near Monterrey, Apr. 26, 1939, *T. C. & E. M. Frye 2490* (U. S. Nat. Herb., no. 1,809,052, TYPE).

This species differs from all *Mateleas* with which I am acquainted because of its white or cream-colored corollas and conspicuous, foliaceous calyx lobes. The extreme reduction of the corona also is noteworthy.

NOTES ON VARIATION IN *TITHONIA TUBAEFORMIS*

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The following notes on variation in *Tithonia tubaeformis* (Jacq.) Cass. were made in S. P. Tlaquepaque, Jalisco, Mexico, where that species grows abundantly along roadways and along the edges of cultivated fields. They were made to supplement the herbarium specimens taken at the same time which have been deposited in the herbarium of the Missouri Botanical Garden.

There is a good deal of variation in form and color from plant to plant as well as on different parts of the same plant. The most conspicuous is in the color of the disk flowers. One form, the commoner, has orange-red on the outside of the disk corollas and on the tips of the chaff of the receptacle. The corolla of the other is dark red, and the difference between the two forms is independent of the age and development of the flower head and is not correlated with the color of the stamens. This same discontinuous variation was noted in other parts of Jalisco.

There is much variation also in the size and shape of the rays and of the involucre bracts. Twenty well-developed plants were examined, and a head terminal to a secondary branch was chosen from each. Heads with about half the disk in flower were selected, eliminating a good deal of the variation caused by different stages of development. Color of disk flowers, number of rays, and length and width of an average ray were recorded for each head. The results are shown in fig. 1. The rays vary from $2\frac{1}{4}$ to $3\frac{1}{2}$ times as long as broad. There is a tendency for many-rayed plants to have smaller rays and for few-rayed plants to have larger rays. In this sample the three plants with dark disks were among those with fewer, larger rays.

Though *Tithonia tubaeformis* is seldom actually planted as an ornamental, it is on the border-line between a cultivated plant and a weed. It comes up in fenced-in gardens and is so often allowed to develop that its orange-yellow flowers are the dominant color note of many little villages in October and November. The seeds apparently are not gathered but the whole plant is frequently cut for coarse hay used in packing, etc.

Figure 1 and the accompanying article are merely a demonstration of the way in which the essential facts regarding variation in a population can be compressed into one diagram which serves as an exact record of the essential facts and a tool in analysis. Selecting flower heads in the manner described removed much of the non-genetic variability. Plant-to-plant variation was then found to be largely concentrated in (1) ray size, (2) ray shape, (3) ray number, (4) corolla color. The inter-relations of all four of these variables are shown in fig. 1. The broken lines for length-breadth proportions have been drawn in as a visual aid in translating position on the chart into ray-shape.

Each circle represents the data from one head, selected one to a plant. Heavy-lined circles represent plants with dark red corollas, the others represent yellow corollas. The figures inside the circles are the number of ray flowers. The position of the circles with regard to the vertical and horizontal scales indicates ray length and breadth respectively.

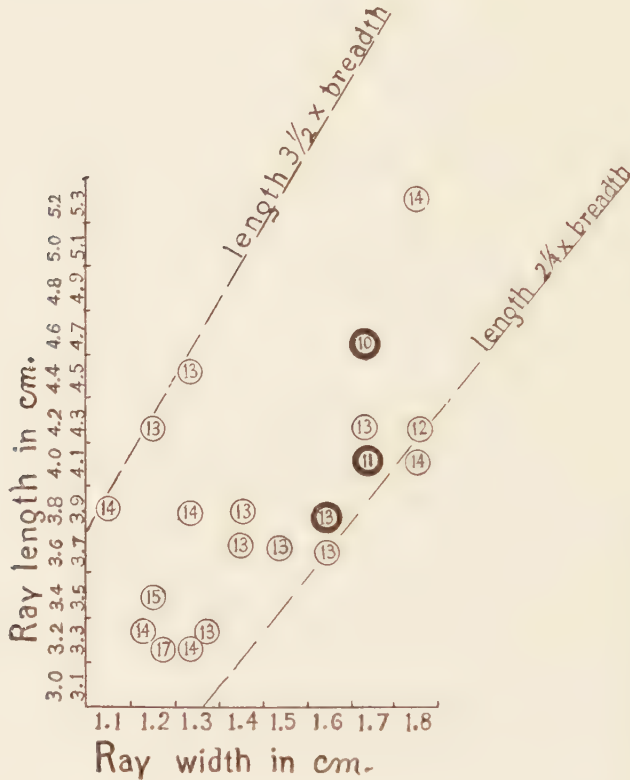


Fig. 1. Variation in ray number, ray length, ray width, and corolla color among 20 plants of *Titbonia tubaeformis* from one locality. Further explanation in the text.

A single chart of this sort is little more than an accurate record of 80 different facts (4 each for 20 plants) and their inter-relationships. A series of such charts for different populations of this species, or comparable charts for other species of *Titbonia*, would allow us to make a real study of evolution in this group of plants. While this method of recording variation was worked out for *Titbonia* it would certainly be quite as effective with the annual species of *Helianthus* and probably with a good many other composites.

A METHOD FOR RECORDING AND ANALYZING VARIATIONS OF INTERNODE PATTERN

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AND DOROTHY SCHREGARDUS

This paper is an attempt "to make measurable that which has not yet been measured," the general habit of a plant. Those systematists who are also good field naturalists are often intrigued by the fact that closely related species of plants are commonly recognizable, even at a distance, by their peculiarities of habit, which are often more reliable than any single characteristic. But habit is difficult to convey to others and difficult to phrase concisely for a key or a technical description. It is based upon a number of things: the size, shape, positions, and textures of the leaves and the internode patterns of the vegetative shoot and the inflorescence. This paper provides an objective means for the analysis of variation in the latter.

Closely related species of the higher plants frequently differ in their internode pattern. That is to say, they may differ from each other not only in the number of internodes and their absolute dimensions but in the relative sizes of successive internodes and *in the pattern of change of relative size*. Unfortunately, there is usually so much variation from plant to plant that examination alone will not suffice to reveal the more or less constant tendencies which are being obscured by individual variation. Differences in internode pattern are apparently brought about largely by growth-regulating influences (of which auxin is certainly only one of several) which proceed from the root, from the stem apex, from leaves, flowers and fruits. The distribution of these substances is under such an internally correlated control system that successive internodes frequently become increasingly smaller or larger in an exact fashion and the increase or decrease may be described in mathematical terms (Prat, '35).

Before internode patterns can be studied, either as an interesting phenomenon in their own right or as a tool in taxonomic, genetic, and physiological investigations, we need a technique for recording and analyzing them. A simple method is presented below which overcomes the inadequacy of the human eye in perceiving rates of change. In fig. 1, for example, there are diagrammed the internodes of four hypothetical stems, A, B, C, and D. Two of these have fundamentally different growth patterns, though that fact will be apparent to relatively few biologists when the data are presented in this fashion. Almost any observant person will immediately note the differences in absolute length and in number of internodes. Most biologists will see the various differences in proportion. Few or none will note the fundamental change in proportion. In all four stems the inter-

nodes are getting increasingly larger but in A and B the increment is itself increasing while in C and D it is decreasing. If, however, we measure the lengths of successive internodes and diagram them from a common base line as in fig. 2, and then connect these points with straight lines for the eye to follow, the change in rate of increase is immediately apparent. A and B produce a fundamentally different curve from C and D.

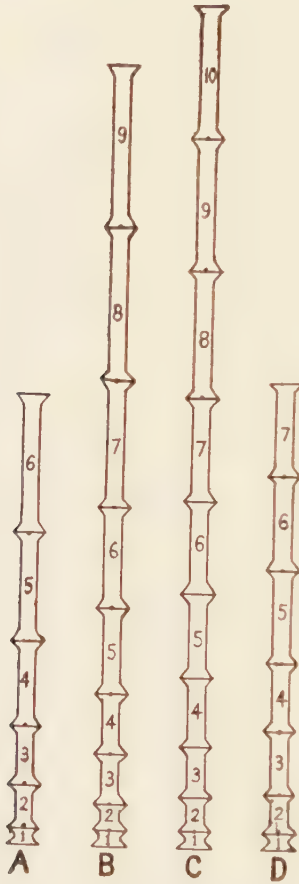


Fig. 1. Nodes and internodes of four hypothetical plants represented diagrammatically but to scale. The internode patterns of A and B are fundamentally different from those of C and D.

The use of logarithmic scales will immediately suggest itself to students of dynamic morphology. Prat ('35) has been successful with this method in analyzing the growth patterns of grass culms, and there are certainly many other kinds of material to which it might be applied. However, the internode patterns

of plants are so various and many of them may be of such complexity that some simple method such as that outlined above should be tried out in each case until the fundamental facts have been established.

The internode pattern differences of two species of *Tradescantia* are illustrated in fig. 3. The method of fig. 2 has been extended by using circles to represent inflorescences and broken lines to represent secondary branches of the main stem (for a more elaborate representation of branching see below). The diagrams were prepared from herbarium specimens, and the small internodes at the base of the stem were ignored, though their pattern is also significant. Figure 3 shows that

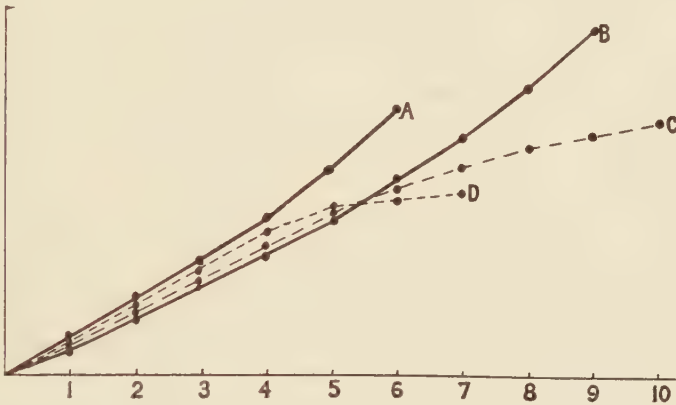


Fig. 2. The data of fig. 1 represented as internode diagrams. Vertical scale, length of internode; horizontal scale, successive internodes. The fundamental difference between A & B and C & D is immediately apparent.

the internode patterns of the two species present a number of out-and-out differences and an even larger number of tendencies to differ. The following are readily demonstrated:

1. *T. subaspera typica* has more internodes.
2. The longest internodes on *T. canaliculata* are usually longer than the longest on *T. subaspera typica*.
3. *T. subaspera typica* has 1 or 2 nodes of increasing magnitude at the base of the stem; *T. canaliculata* has 2 to 5.
4. The terminal internodes of *T. subaspera typica* decrease regularly in length. The decrease is so regular that the graph tends very strongly to be a straight line and might be described mathematically in exact terms. *T. canaliculata* has no such tendency; the terminal internodes may or may not be somewhat shorter than those preceding them.

The diagrams of fig. 3 illustrate several other significant points. *T. canaliculata* is a ubiquitous weed over a wide territory (Anderson and Woodson, '35). It in-

cludes a number of more or less differentiated races or sub-species which were once probably quite distinct but whose characters and distributions have been greatly modified by civilization (Anderson and Hubricht, '38). The three diagrams in the center of the figure represent one of these vaguely defined races in Texas and Oklahoma. *T. subaspera typica* and *T. canaliculata* sometimes hybridize when man so distorts the natural balance of things that hybrids can be produced and can find an intermediate habitat in which to survive (Anderson and Hubricht, '38,

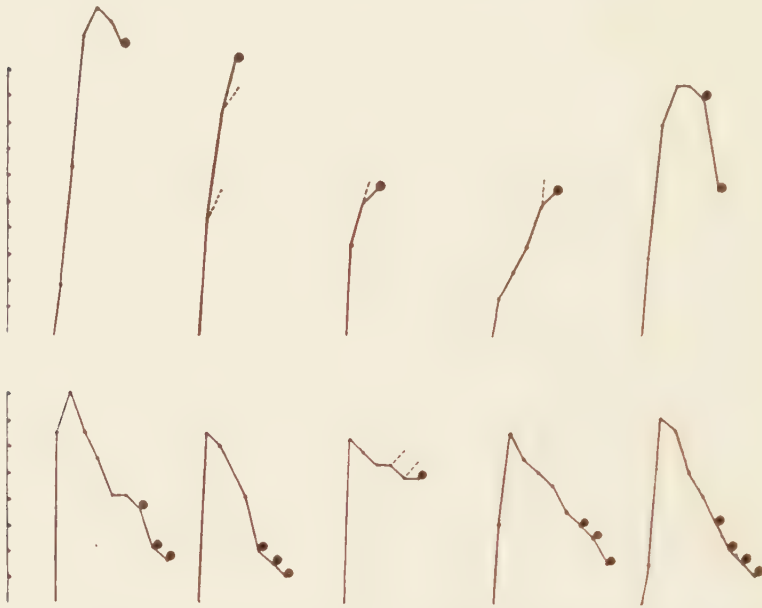


Fig. 3. Internode diagrams of five plants of *Tradescantia canaliculata* (above) and *T. subaspera* var. *typica* (below). Circles represent inflorescences and dotted lines represent branches. Each division on the scale at the left equals two centimeters.

Hubricht and Anderson, '41). One of the plants of *T. subaspera typica* came from such a habitat and was collected only a few feet from an apparent F_1 hybrid between the two species. While in its other characters it shows little influence of *T. canaliculata*, its internode pattern is so different that several biologists who have been shown these diagrams have been able to pick out the plant immediately. It is the third from the left in fig. 3.

Internode diagrams are particularly useful in analyzing such natural populations in which hybridization has occurred but in which it is not evident whether it is a blind alley or whether the variability of one or the other of the parental species is being enriched by back-crossing. Even in those cases where the parental species

are so strikingly different that first-generation hybrids can be identified by inspection, it is a very difficult discipline so to train the eye that possible back-crosses can be distinguished. Unanalyzed variation in internode lengths gives the observer a vague impression as to the degree of variation but it usually does not answer the much more important question of its *direction*. Figure 4 illustrates a case in point, the hybridization between two species of Sage recently discussed by Epling ('44, pl. 4). Numerous individuals of both species and occasional undoubted



Fig. 4. Internode diagrams of two species of *Salvia* from Mt. Wilson, California, and a suspected back-cross hybrid. Same scale as fig. 3.

hybrids between them were studied along the Mt. Wilson road. At various points near well-established hybrids there were peculiar plants of *Salvia mellifera* but even Dr. Epling was unable to determine whether the variation was in the direction of *S. apiana*, as we would expect if the peculiarities were due to back-crossing.

Figure 4 suggests that the two species differ by the number of internodes below the flower, by the number of flowering nodes, and by whether the terminal internode is much longer than the one below it or of about the same size. It will be seen that in all of these characters the queer-looking individual departs from normal *S. mellifera* in the direction of *S. apiana*. The evidence from internode pattern would therefore suggest that it arose as a back-cross between *S. mellifera* and the first-generation hybrid which was growing near by. The internode diagrams (of which those in fig. 4 are a small sample) not only answered this question; they defined the internode differences between the two species so exactly that it was possible to study variation within and between these two species with a precision and an understanding hitherto impossible.

Sometimes the internode patterns of the secondary stems or of the inflorescences may be more significant than those of the main stem. They may then be diagrammed separately or combined in various ways. After a number of trials the technique shown in fig. 5 has apparently the widest applicability. It diagrams two plants each of two species of *Tripsacum*. The secondary branches are diagrammed

from a new base line immediately above the node at which they originate and the tertiary branches from a still higher base line. The tertiaries of *T. Lemmoni* were too short at the time the measurements were made to register on the scale and are therefore indicated as short vertical lines of the approximate number of internodes.

The method described above might prove useful in a number of ways. Its prime importance will be to the student who is trying to understand specific or racial differences as well as to describe them. A monographer working in the field



Fig. 5. Internode diagrams of two plants of *Tripsacum dactyloides* (left) and two of *T. Lemmoni* (right). Scale and construction as in figs. 3 and 4. The main axes of the four plants are diagrammed on line I, the secondary branches on line II and the tertiary branches (when present) on line III. The dotted lines for the tertiaries of *T. Lemmoni* represent short sterile branches of one to three nodes too short to be shown on the same scale as the rest of the diagrams.

of pure taxonomy would probably have little to learn from this method. Only in exceptional instances will it reveal a clear-cut specific difference which can be neatly phrased in a few words and incorporated in the description of a species or used in a key. However, the student of the species problem will find such characters as internode pattern of prime importance. His job is not merely to discriminate species but to illuminate them (Epling, '44, Anderson and Ownbey, '39, Anderson and Whitaker, '34). He must go beyond the cataloguing of a few outstanding differences and attempt to comprehend how the hiatus between two species came into being and how it is maintained. Internode patterns are reflections of internal growth-regulating systems. A comparison of patterns in different species or races may give us a real insight into the dynamics of these differences. The simple method outlined above may actually bring us closer to understanding fundamental physiological differences than would a series of chemical analyses. In this way it might be generally useful in various theoretical and practical problems.

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A MONOGRAPHIC STUDY OF THE GENUS *PALAFoxia* AND ITS IMMEDIATE ALLIES¹

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INTRODUCTION

It has been the purpose of this study to evaluate taxonomically on the basis of morphological examination the generic and specific entities involved in *Palafoxia* and its immediate allies, southern United States and Mexican representatives of the tribe Helenieae in the Compositae. Early in the history of the group considered, it was recognized that more than one generic element was present in this complex of related plants, but the exact nature and scope of these units were not known. There have been many different interpretations of the generic relationships and considerable shifting of the species from one genus to another without satisfactory results.

From the present study it is concluded that there are three distinct genera in the group, namely, *Othake*, *Polypteris*, and *Palafoxia*, and that in the last genus two elements are enough different to substantiate division into two subgenera.

The second part of this problem has been to determine the generic relationships of the species involved and to examine their validity. In *Othake* delimitation of the species has been unsatisfactory because of the great variability of the plants; certain species have been based on specimens which more thorough collecting proves to be extreme forms scarcely equal in rank to the recognized entities. It has therefore seemed advisable to reduce two species to varietal rank and to place another in synonymy. A somewhat similar situation in *Palafoxia* warrants the reduction of a species to a variety.

Morphological examination was based on herbarium material in the Missouri Botanical Garden and on living material observed and collected in Texas by the writer. Type specimens and additional material were obtained from the Gray Herbarium, the Academy of Natural Sciences of Philadelphia, the New York Botanical Garden Herbarium, and the S. M. Tracy Herbarium of A. and M. College, College Station, Texas.

It is with sincere appreciation that the kindness and assistance of Dr. Jesse M. Greenman is acknowledged. To Dr. George T. Moore, for the facilities of the library and the herbarium, and to Mr. H. B. Parks, for many specimens from Texas, thanks are also expressed.

¹ An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of master of science in the Henry Shaw School of Botany of Washington University.

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TAXONOMIC HISTORY

Since it would be impossible to relate the history of any one of these three genera without continually referring to that of the other two, it seems best to present as a single unit the changing historical positions and inter-relationships of the genera concerned.

Palafoxia, named for the Spanish general, José Palafox, was the first genus of this complex to be described. In 1816 Lagasca¹ gave this name to a plant from "New Spain," which was grown in the Royal Gardens at Madrid and which Cavanilles had at first called *Ageratum lineare*² and afterwards transferred to *Stevia*³. Later in the year 1816 Cassini published the genus *Paleolaria*⁴, based on Lagasca's plant, but did not actually describe the type species until 1818. At that time he placed *Palafoxia linearis* in synonymy under his *Paleolaria carnea*⁵, which, along with the generic name, cannot be retained because of the priority of the earlier name.

With the publication of the genus *Polypteris*⁶ together with its Floridian type species, *P. integrifolia*, by Nuttall in 1818, an element closely related to the first-mentioned plant was introduced. The similarity caused Lessing⁷ in his 'Synopsis Generum Compositarum' to include both genera under *Paleolaria*, which he recognized in preference to *Palafoxia*. Regarding the species, he says, "*Paleolaria carnea* Cass. = *Palafoxia linearis* Lag." and "*Paleolaria fastigiata* Less. = *Polypteris integrifolia* Nutt."

The next allied plant recorded in the literature was from Arkansas and was described by Nuttall as *Stevia callosa*⁸ in 1821. DeCandolle⁹, in his 'Prodromus' (1836), transferred this species to *Florestina* and included under the genus *Palafoxia*: *P. linearis*, *Polypteris integrifolia* as *Palafoxia fastigiata*, in addition to two new species. Under the name *Polypteris integrifolia* Nutt. he placed a plant with entirely different generic affinities.

In 1836 also Rafinesque¹⁰ based a new genus on Nuttall's *Stevia callosa* and named the entity *Othake*, separating it from existing genera chiefly on the nature of the involucre bracts and the "deep-cut florets." This name was not employed till later, however, for the species involved were for some time referred to *Palafoxia*, *Polypteris*, or distributed between the two genera.

¹ Lag. Elench. Pl. Hort. Matr. 26. 1816.

² Cav. Ic. 3:3, t. 205. 1794.

³ Cav. Praelect. n. 464, and Ic. 4:32. 1797.

⁴ Cass. in Bull. Soc. Phil. 198. 1816.

⁵ Cass. in Bull. Soc. Phil. 47. 1818.

⁶ Nutt. Gen. N. Am. Pl. 2:139. 1818.

⁷ Less. Syn. Comp. 155. 1832.

⁸ Nutt. in Jour. Acad. Nat. Sci. Phila. I. 2:121. 1821.

⁹ DC. Prodr. 5:124, 655, 659. 1836.

¹⁰ Raf. New Fl. Am. 4:73. 1836.

Torrey and Gray¹¹, in 1842, united the scattered, related elements under three sections of the single genus *Palafoxia*: 1. *Eupalafoxia*, 2. *Florestinaria*, and 3. *Polypteris*. Bentham and Hooker¹², in 1873, followed the same interpretation and located *Palafoxia* in the subtribe Baerieae of the tribe Helenioideae.

In 1883 Dr. Gray¹³ maintained that the separation of *Palafoxia* and *Polypteris* was substantiated by the nature of the involucre bracts and the corolla characters. Nuttall's *Stevia callosa*, with its immediate allies, and *P. integrifolia* were referred to the genus *Polypteris*; *Palafoxia linearis* and the anomalous Floridian species, *P. Feayi*, were retained in *Palafoxia* and included in the Helenieae of the Helenioideae. Hoffmann's¹⁴ treatment of the Compositae (1891) reunited all of the entities under *Palafoxia*.

The first monographic study of the Texas and southwestern representatives of the complex was made in 1904 by Bush¹⁵. He recognized Rafinesque's name, *Othake*, for the greater number of the species in the *Polypteris* group of Gray and applied the latter name to the original type-species only, *P. integrifolia*. The most complete monographic investigation has been that of Rydberg¹⁶, who recognized three genera, *Polypteris*, *Othake*, and *Palafoxia*, and placed them in a separate subtribe, Palafoxianae.

GENERAL MORPHOLOGY

Roots.—In *Polypteris* the numerous, slender, fibrous roots develop from a short, stout woody base of perennial duration. *Othake* and *Palafoxia* have annual taproots which may become woody and perennial under conditions favoring continued growth.

Stems.—In these three genera the stems are herbaceous throughout or suffrutescent, but never entirely ligneous. The stems of *Polypteris* are either simple or sparingly branched below the inflorescence; those of *Palafoxia* are extensively branched throughout; both of these conditions are represented by the species of *Othake*. In the nature of the pubescence and the glandular element the genera differ. In *Polypteris* the stem is strigillose and eglandular, while the stems of *Othake* and *Palafoxia*, with a few exceptions, are strigose-hirtellous or strigose-hirsute and densely glandular above.

Leaves.—The leaves in the three genera are quite similar, being alternate or the lower ones opposite, and usually narrowed at the base into a short petiole; they vary in shape from linear to ovate-lanceolate and are entire. Three nerves are usually visible, or the two fainter lateral ones may be indistinct because of the dense pubescence. A small, yellowish callosity is found at the apex.

¹¹ Torr. & Gray, Fl. N. Am. 2:368. 1842.

¹² Benth. & Hook. Gen. Pl. 2:405. 1873.

¹³ Gray in Proc. Am. Acad. 19:30. 1883.

¹⁴ Hoffm. in Engl. & Prantl, Die Nat. Pflanzenfam. IV, Abt. 5, p. 261. 1891.

¹⁵ Bush in Trans. Acad. Sci. St. Louis 14:173. 1904.

¹⁶ Rydb. in N. Am. Fl. 34:58. 1914.

Pubescence.—The hairs on the vegetative parts of these plants are multicellular, tuberculate, and usually coarse. *Othake* is characterized by a strigose-hirtellous type of indument, which is found on the stems, leaves, and involucre. The peculiar type of capitate, glandular hair found among the other hairs in *Othake* is best illustrated in *O. callosum*, where the large, mushroom-shaped structures with purplish glandular caps are conspicuous. The hair bases and adjacent cells are usually distended and somewhat glandular. In *Palafoxia* the pubescence is similar but more hispid, and the glandular hairs have larger bases and smaller glandular tips. *Polypteris* is strigillose and eglandular.

Inflorescence.—In *Polypteris* there is a single corymbiform cluster of many discoid heads terminating the stem. In *Palafoxia* cymose or corymbiform clusters of a few discoid heads are borne at the ends of the branches. In *Othake* both of these conditions occur, and the heads are either discoid or radiate.

Involucre.—The involucre bracts are 2–3-seriate, but in other characteristics they are strikingly different in the three genera. In *Polypteris* the bracts are papery and membranaceous; they are flat, obtuse to truncate, almost glabrous, and several of the shorter outer bracts are reflexed. The bracts of *Othake* are herbaceous, densely pubescent, often glandular, with an irregular, dry, reddish tip, and at times show a tendency to embrace the marginal achenes at maturity. In the typical *Palafoxia* the involucre is entirely herbaceous and glandular-pubescent, the bracts being acute, subequal, keeled, and closely clasping the mature marginal achenes. In the last two genera the innermost bracts are often narrowed, thin, and hyaline-margined. The involucre of *Othake* and *Polypteris* are turbinate, while those of *Palafoxia* are oblong-conic.

Receptacle.—A small, flat, naked and pitted receptacle with irregular aggregations of tissue around the base of the achenes is characteristic of all three genera.

Corollas.—The nature of the corolla separates *Othake* and *Polypteris* from *Palafoxia*. In *Palafoxia* the floret has a long, cylindraceous throat which exceeds the 5 short lobes and tube. *Polypteris* and *Othake* have florets with 5 long, spreading lobes, a filiform tube, and a short campanulate throat, which in *Othake* is often indistinguishable. The lobes in all the genera are usually thickened at the tip, puberulent without, and minutely papillose on the inner surface of the entire lobe. The tube is glabrous, puberulent, or glandular-puberulent, and dilated at the base. The ray florets of the heterogamous species of *Othake* are pistillate, fertile, and have deeply 3-lobed ligules. The style branches are revolute or spreading, papillose to hispidulous on the outer surface, and with 2 stigmatic lines on the inner faces. In color the florets vary from flesh to rose.

Achenes.—The achenes of *Polypteris* are 4–5-angled with unequal faces. Those of *Othake* and *Palafoxia* are square in cross-section. In *Polypteris* and *Othake*, the achenes are obpyramidal and often arcuate because of the pressure of adjacent achenes; in *Palafoxia* they are linear or somewhat obpyramidal and straight. Only one species in the group has glabrous achenes, *O. Lindenii*; in the

others, the degree of pubescence varies from hirsute to puberulent.

Pappus.—The pappus-scales vary greatly in the three genera and exhibit both generic and specific differences, but the same general type of scale is present throughout, namely, a callose midrib, broad at the base and narrowed upward, with scarious, hyaline margins. In *Polypteris* and *Othake* the midrib is slender and does not exceed the throat in length, while in *Palafoxia* it is stiff and broad and almost the length of the corolla. In *Othake* the length and shape of the scale and the nature of the apex assist in differentiating the species; also, in certain species with homogamous heads, the pappus-scales of the marginal florets are often reduced, as they are consistently in the ray florets of the heterogamous heads.

GEOGRAPHICAL DISTRIBUTION

The representatives of this group are found chiefly in Florida and the southwestern United States. *Polypteris* is limited in its distribution to Florida and southern Georgia. Species of *Othake* have their center of distribution in Texas but extend northeast to Missouri, south to Mexico, and northwest to Colorado. *Palafoxia* is represented in Florida by one species, and the remainder of the genus occurs in southwestern United States and Mexico.

ABBREVIATIONS

The herbaria from which specimens have been cited are indicated by the following abbreviations: Missouri Botanical Garden (MBG); Herbarium of the Academy of Natural Sciences, Philadelphia (ANSP); Gray Herbarium of Harvard University (G); Herbarium of the New York Botanical Garden (NYB); S. M. Tracy Herbarium of the A. and M. College, College Station, Texas (SMT).

TAXONOMY

KEY TO THE GENERA

- | | |
|---|------------|
| A. Heads radiate or discoid; lobes and tube of the corolla much longer than the throat. | |
| B. Involucral bracts herbaceous with membranaceous, reddish tips..... | OTHAKE |
| BB. Involucral bracts membranaceous and papery, sub-stramineous..... | POLYPTERIS |
| AA. Heads discoid; lobes and tube of the corolla much shorter than the throat..... | PALAFOXIA |

OTHAKE

Othake Raf. New Fl. Am. 4:73. 1836; Bush in Trans. Acad. Sci. St. Louis 14:173. 1904; Wooton & Standley in Contrib. U. S. Nat. Herb. 19:722. 1915; Rydb. in N. Am. Fl. 34¹:58. 1914, Fl. Rocky Mts. & Adj. Plains, 944. 1917, and Fl. Prairies & Plains Cent. N. Am. 854. 1932.

Stevia Nutt. in Jour. Acad. Nat. Sci. Phila. 2:121. 1821, not *Stevia* Cav. Ic. 4:32, t. 342-356. 1797.

Palafoxia DC. Prodr. 5:124. 1836, in part, not *Palafoxia* Lag. Gen. et Sp. Nov. 26, 1816; Torr. & Gray, Fl. N. Am. 2:368. 1842, in part; Benth. & Hook.

Gen. Pl. 2:405. 1873, in part; Hoffm. in Engl. & Prantl, Die Nat. Pflanzenfam. IV, Abt. 5, p. 261. 1891.

Florestina DC. Prodr. 5:655. 1836, in part, not *Florestina* Cass. in Bull. Soc. Phil. 175. 1815.

Polypteris Gray in Proc. Am. Acad. 19:30. 1883, in part, and Syn. Fl. N. Am. 1²:74, 337. 1884, and ed. 2. 1886, in part; Chapman, Fl. South. U. S., ed. 3, 261. 1897, in part; Small, Fl. Southeast. U. S., 1287. 1903, and ed. 2, 1913, in part; Gray, Manual, ed. 7, 843. 1908.

Herbaceous, caulescent annuals, occasionally woody at the base and perennial. Stem usually solitary from a stout tap-root, branched, strigose, usually glandular above. Leaves alternate or the lower opposite, entire, thick, 1-3-nerved. Heads discoid or radiate in corymbiform clusters terminating the branches. Involucre turbinate, the bracts in 2-3 series, subequal, the somewhat shorter outer bracts not reflexed, herbaceous and green with a sphacelate, reddish tip, and tending occasionally to enfold the marginal achenes. Receptacle flat, naked, and pitted. Corollas reddish-pink, those of the disc-florets perfect, regular, deeply 5-lobed, the lobes and filiform tube at least twice as long as the short, campanulate throat. Ray-florets, when present, in one cycle, pistillate and fertile, deeply 3-lobed. Stamen-tube completely exerted, the anthers obtuse at the base. Style-branches linear, spreading or revolute, hispidulous. Achenes 4-angled, obpyramidal. Pappus of 7-10 scales, varying from a minute callosity to a long, acuminate, hyaline-margined callose midrib exceeding the corolla-tube, the squamallae of the ray-florets of the radiate heads and often of the marginal florets of the discoid heads reduced.

Type species: *Othake tenuifolium* Raf. New Fl. Am. 4:73. 1836 (= *Othake callosum* (Nutt.) Bush).

KEY TO THE SPECIES

A. Heads discoid.

B. Pappus-scales 0.5-3.0 mm. long, exceeded by the achenes, the scales of the marginal achenes not reduced in size.

C. Pappus-scales less than 1.5 mm. long, obtuse; florets 7-12 in a head; leaves 1-2 mm. wide

1. *O. CALLOSUM*

CC. Pappus-scales 2-3 mm. long, acute or obtuse; florets 12 or more in a head; leaves more than 3 mm. wide.

D. Plants slender, florets 12-20 in a head; leaves 3-5 mm. wide ... 2. *O. ROSEUM*

DD. Plants stout, florets about 25, occasionally more, leaves 0.7-1.5 cm. wide

2a. *O. ROSEUM* var.
ROBUSTUM

BB. Pappus-scales 3.5-8.0 mm. long, equalling or exceeding the achenes, rarely shorter, the scales of the marginal achenes often reduced in size.

E. Achenes distinctly pubescent.

F. Pappus-scales acute, 3.5-4.5 mm. long, peduncles sparingly glandular-pubescent.....

3. *O. TEXANUM*

FF. Pappus-scales acuminate, 6-8 mm. long, peduncles distinctly glandular-pubescent.....

3a. *O. TEXANUM* var.
MACROLEPIS

EE. Achenes glabrous, or nearly so..... 4. *O. LINDENII*

AA. Heads radiate.

- G. Plants slender; leaves linear, 2–6 mm. wide, florets 9–12 in a head 5. *O. REVERCHONII*
 GG. Plants stout, leaves lanceolate, 0.5–1.5 cm. wide, florets 20–70 in a head.
 H. Stem branched, florets 20–30, glandular-pubescent on the peduncles only 6. *O. SPHACELATUM*
 HH. Stem simple, florets 60–70, the entire plant usually glandular-pubescent and somewhat viscid 7. *O. HOOKERIANUM*

1. *Othake callosum* (Nutt.) Bush in Trans. Acad. Sci. St. Louis **14**:174. 1904; Britt. & Brown, Illust. Fl. **3**:507, fig. 4535. 1913; Rydb. in N. Am. Fl. **34**¹:59. 1914.

Othake tenuifolium Raf. New Fl. Am. **4**:74. 1836.

Stevia callosa Nutt. in Jour. Acad. Nat. Sci. Phila. I. **2**:121. 1821, and in Linnaea **4**:40. 1829; Barton, Fl. N. Am. **2**:31, t. 46. 1822.

Florestina callosa DC. Prodr. **5**:655. 1836.

Palafoxia callosa (Nutt.) Torr. & Gray, Fl. N. Am. **2**:369. 1842; Walp. Rep. Bot. Syst. Suppl. **1**:949. 1843.

Polypteris callosa (Nutt.) Gray in Proc. Am. Acad. **19**:30. 1883, and Syn. Fl. N. Am. **1**²:337. 1884, and ed. 2. 1886; Coulter in Contrib. U. S. Nat. Herb. **2**:230. 1892.

A slender, herbaceous annual; stem 1–5 dm. high, somewhat geniculate, terete, canescent-strigose, finely furrowed, somewhat shining below; leaves sessile or nearly so, linear to lanceolate-linear, 3–5 cm. long, 1–2 mm. broad, obtuse, narrowed at the base, strigose and hispidulous on both surfaces, 1(–3)-nerved; peduncles slender, minutely strigose, densely glandular-pubescent with large purple-tipped hairs; heads numerous, about 1 cm. high; involucre bracts 7–9, linear to oblong-lanceolate, about 5 mm. long, acute to acuminate, slightly fimbriate at the apex, strigose, eglandular or with a few capitate-glandular hairs; florets 7–12 in a head; corolla-lobes linear, 3.5 mm. long, obtuse to acutish, the tips pubescent without; throat campanulate, very short, about 0.5 mm. long, glabrous; tube slender, somewhat expanded at the base, 2.0–2.5 mm. long, pubescent, sparingly glandular; achenes 3–4 mm. long, puberulent; pappus-scales 8–9, subequal, varying from a minute, blunt, callose midrib to a broadly ovate scale 1 mm. or less long, with an erose hyaline margin and a glabrous included rib.

Distribution: southern Missouri to Texas.

MISSOURI: Greene Co., Sept. 4, 1893, *Bush 203* (MBG); Eagle Rock, Barry Co., Sept. 17, 1896, *Bush 115* (MBG); barrens, Swan, Sept. 24, 1899, *Bush 476*, and Sept. 22, 1905, *3354* (MBG); barrens, Eagle Rock, Aug. 9, 1905, *Bush 3187* (MBG); gravelly bars, Noel, Aug. 7, 1908, *Bush 4983* (MBG); barrens, Barry Co., July 16, 1935, *Bush 14999* (MBG); dry ground, Baxter, Sept. 10, 1935, *Bush 15180* (MBG); gravelly places, Barry Co., Sept. 10, 1935, *Bush 15190* (MBG); rocky banks, Stone Co., Sept. 11, 1935, *Bush 15195* (MBG); bottoms, Barry Co., Sept. 22, 1936, *Bush 15756* (MBG); common in barrens, Eagle Rock, Barry Co., Sept. 17, 1898, *Mackenzie* (MBG); gravelly bars, Noel, Aug. 7, 1908, *Palmer 4893*, Sept. 2, 1913, *4078*, and Sept. 11, 1920, *19067* (MBG); rocky ledges, barrens, Galena, Stone Co., Oct. 11, 1913, *Palmer 4633* (MBG); rocky

terraces of "bald knobs," Roark, Stone Co., Sept. 28, 1920, *Palmer 19204* (MBG); sandstone glades, top of bluff along river, near Tecumseh, Ozark Co., Oct. 8, 1927, *Palmer 33012* (MBG); Wilson Creek, Green Co., *Shepard* (MBG); upland open places bordering limestone glade, 2 mi. w. of Richville, Douglas Co., Aug. 19, 1934, *Steyermark 14657* (MBG).

ARKANSAS: barrens, Benton Co., Sept. 9, 1936, *Bush 15752* (MBG); barrens, Oakgrove, Oct. 7, 1936, *Bush 15942* (MBG); along railroad track, Gilbert, Searcy Co., Aug. 5, 1913, *Emig 43* (MBG); without definite locality, *Nuttall* (ANSP), TYPE; Red River, *Nuttall* (ANSP); barrens, rocky hillsides, Beaver, Carroll Co., Sept. 26, 1913, *Palmer 4492* (MBG); Eureka Springs, Aug. 1887, *Wislizenus* (MBG).

OKLAHOMA: roadside clay soil, 6 mi. s. of Elk City, Beckham Co., Oct. 17, 1936, *Eskeu 1502* (MBG).

TEXAS: rocky soil, s. of San Antonio, Bexar Co., June 25, 1938, *Ammerman 8*, and rocky soil near Kerrville, June 30, 1938, *39* (MBG); Dallas, common on hills, Sept. 26, 1900, *Bush 1146*, and common in barrens, Oct. 30, 1900, *1635* (MBG); 1.5 mi. n. of Leona, Leon Co., Oct. 5, 1937, *Cory 25366* (MBG); dry hills in Jacksonville, Cherokee Co., Aug. 29, 1898, *Eggert* (MBG); between Sheffield and Pecos River, Pecos Co., July 23, 1921, *Ferris & Duncan 2915* (MBG); sandy woods and fields, Dallas, June 20, 1872, *Hall 356* (MBG); Willow Creek, Gillespie Co., *ex Herb. Jermy 804* (MBG); Denison, July 22-25, 1880, *Letterman* (MBG); Comanche Spring, Nov. 1849, *Lindheimer 956*, and New Braunfels, 1851, *955* (ANSP, MBG); dry, calcareous soil, Comanche Peak near Granbury, Hood Co., Sept. 15, 1914, *Palmer 6443a* (MBG); rocky open ground, Kerrville, Kerr Co., Oct. 5, 1916, *Palmer 10898* (MBG); gravel bars of river, Blanco, Blanco Co., Sept. 24, 1917, *Palmer 12856* (MBG); dry, calcareous open ground, near Brownwood, Brown Co., Nov. 1, 1925, *Palmer 29531* (MBG); Bexar Co., Sept. 8, 1938, *Parks* (MBG); 1.5 mi. w. of Mountain Home, Kerr Co., Oct. 1, 1936, *Parks & Cory 20747 & 20748* (SMT); dry ground, Dallas, Oct. 1, 1902, *Reverchon* (MBG); dry uplands, Oak Cliff, Oct. 16, 1902, *Reverchon 3288* (MBG); limestone prairies, Dallas, Oct. 16, 1902, *Reverchon* (MBG); on rocks, Comanche Peak, Sept. 1903, *Reverchon 3655* (MBG); Weatherford, Oct. 18, 1902, *Tracy 8142* (MBG).

2. *Othake roseum* Bush in Trans. Acad. Sci. St. Louis 14:175. 1904; Rydb. in N. Am. Fl. 34¹:59. 1914.

Polypteris rosea (Bush) Small, Fl. Southeast. U. S., ed. 2, 1372. 1913.

A slender, herbaceous annual; stem 3-6 dm. high with a few ascending branches, terete, strigose, somewhat scabrous, finely furrowed, cinereous; leaves petiolate, linear-lanceolate, 4-6 cm. long, 3-5 mm. broad, obtuse, narrowed at the base, scabrous on both surfaces, 1(-3)-nerved; peduncles slender, long, finely glandular; involucre bracts 7-10, oblanceolate, 6-8 mm. long, acute to obtuse, strigose, eglandular; florets 12-20 in a head; corolla-lobes linear, 4 mm. long, the tips pubescent without; throat campanulate, very short, about 0.5 mm. long, glabrous; tube slender, dilated at the base, 4 mm. long, minutely glandular-puberulent; achenes 3-4 mm. long, pubescent; pappus-scales about 8, ovate-lanceolate, about 2 mm. long, acute or obtuse, the midrib dorsally pubescent, the hyaline margins erose, scales of the marginal achenes scarcely reduced.

Distribution: Texas.

TEXAS: about 2 mi. s. of College Station, Brazos Co., June 22, 1938, *Ammerman 7* (MBG); Houston, Oct. 25, 1900, *Bush 1599* (MBG); sandy ground near Dallas, June 24, 1899, *Eggert* (MBG); along Devils River, Valverde Co., Sept. 10, 1900, *Eggert* (MBG); Dallas, June 16, 1898, *Glatfelter* (MBG); Galveston Bay, Sept. 26, 1884, *Joor* (MBG);

banks of Buffalo Bayou, near Houston, Oct. 1841, *Lindheimer* (MBG); wet prairies, Houston, Aug. 1842, *Lindheimer* (MBG); dry open ground, Houston, Harris Co., Sept. 16, 1915, *Palmer* 8575 (MBG); prairies, Bryan, Brazos Co., Sept. 17, 1916, *Palmer* 10732 (ANSP, MBG); College Station, Brazos Co., July, 1888, *Pammel* (MBG); Newland, near Dallas, June 6, 1901, *Reverchon* 2577, and sands, Dallas, May 1, 1902, 3290 (MBG); Buzzards Spring, Aug. 7, 1902, *Reverchon* 3290 (MBG); Sheldon, Sept. 20, 1903, *Reverchon* 3656, and Oct. 7, 1903, 3656 TYPE (MBG); Millett, Nov. 4, 1897, *Trelease* (MBG); Willis, Aug.-Sept., *Warner* (MBG).

2a. *Othake roseum* var. *robustum* (Rydb.) Ammerman, comb. nov.

O. robustum Rydb. in N. Am. Fl. 34¹:60. 1914.

Polypteris robustum (Rydb.) Cory in *Rhodora* 38:408. 1936.

Stem 3–7 dm. high, stout, often ligneous below; leaves lanceolate to ovate-lanceolate, 4–8 cm. long, 0.7–1.5 cm. wide, indistinctly 3-nerved; peduncles glandular; florets about 25, occasionally more, in a head; as the species in other characters.

Distribution: southern Texas, south to Tamaulipas, Mexico.

TEXAS: Corpus Christi Bay, Nueces Co., *Heller* 1562 (MBG); Highway 35, Aransas Co., Highway 181, Bee Co., and Highway 181, Bexar Co., Sept. 9, 1938, *Parks* (MBG); Karnes Co. and Refugio Co., Sept. 9, 1938, *Parks* (MBG); Highway 181, San Patricio Co., and Highway 77, Victoria Co., Sept. 9, 1938, *Parks* (MBG); Wilson Co., Sept. 8, 1938, *Parks* (MBG); 12 mi. s. e. of Hebbronville, Jim Hogg Co., Oct. 7, 1935, *Parks* & *Cory*, 16941 & 16942 (SMT); seashore at Rockport, July, 1893, *Reverchon* 1230 (MBG); Brownsville, Aug. 1, 1923, *Runyon* 209 (MBG).

MEXICO:

TAMAULIPAS: dunes, Tampico, Nov. 24, 1937, *Kenoyer* 728 (MBG); vicinity of Tampico, Jan. 1–31, 1910, *Palmer* 38 (MBG); sand-dunes of Gulf coast, Tampico, July 4, 1896, *Pringle* 6354 (MBG), CO-TYPE.

3. *Othake texanum* (DC.) Bush, Trans. Acad. Sci. St. Louis 14:176. 1904; Rydb. in N. Am. Fl. 34¹:59. 1914; Wootton & Standley, Contrib. U. S. Nat. Herb. 19:722. 1915.

O. canescens Rydb. in N. Am. Fl. 34¹:60. 1914.

Palafoxia Texana DC. Prodr. 5:125. 1836, not Hook. Ic. Pl. t. 148. 1837; Dietrich, Syn. Pl. 1345. 1847; Torr. & Gray, Fl. N. Am. 2:369. 1842; Hemsli. Biol. Cent.-Am. Bot. 4:59. 1886.

Polypteris Texana (DC.) Gray in Proc. Am. Acad. 19:30. 1883, and Syn. Fl. N. Am. 1²:337. 1884, and ed. 2. 1886; Small, Fl. Southeast. U. S., 1287. ed. 1. 1903, and ed. 2. 1913.

An herbaceous, rather stout annual, occasionally woody below and perennial; stem 3–5 dm. high, much-branched, terete, strigose, shallowly furrowed; leaves petiolate, linear-lanceolate to ovate-lanceolate, 3–5 cm. long, 0.3–1.0 cm. broad, obtuse, strigose on both surfaces, narrowed or somewhat rounded at the base, 3-nerved, petiole 4–6 mm. long; peduncles rather stout, strigose and somewhat glandular, but not densely so; heads numerous, 1.0–1.5 cm. high; involucrel bracts 12–15, linear-lanceolate, acute to obtuse, about 9 mm. long, strigose, eglandular; florets 25–30 in a head; corolla-lobes linear, 3–4 mm. long, the tips pubescent without; throat short, campanulate, about 0.5 mm. long; tube slender,

dilated at the base, about 3 mm. long, finely glandular-pubescent; achenes 4.5–6.0 mm. long, pubescent; pappus-scales 6–8, obovate, 3.5–4.5 mm. long, acute, erose, the midrib dorsally pubescent, the pappus of the outer achenes shorter, 1.0–1.5 mm. long, and obtuse.

Distribution: Oklahoma, Texas, and northern Mexico.

OKLAHOMA: Johnson's Pasture, McClain Co., June 26, 1937, *Barkley 1499* (MBG); vicinity of Fort Sill, July 14, 1916, *Clemens 11844* (MBG).

TEXAS: south of San Antonio, Bexar Co., June 18, 1938, *Ammerman 97* (MBG); from Laredo to Bexar, *Berlandier 604, 2014* co-TYPE (MBG); in low area, 1 mi. e. of Cotulla, LaSalle Co., July 30, 1921, *Ferris & Duncan 3014* (MBG); escarpment of Staked Plains on Quitaque-Plainview Rd., Floyd Co., Aug. 23, 1921, *Ferris & Duncan 3375* (MBG); Spofford, May 8–9, 1904, *Griffiths 6320* (MBG); Del Rio, April 21, 1930, *Jones 26398*, Carriso Spring, April 26, 28008, and Laredo, March 24, 1932, *29467* (MBG); sandy bluffs near Laredo, Aug., 1899, *Mackenzie 7* (MBG); Laredo, Feb. & March, *Orcutt 5548* (MBG); sandy, open ground, Pleasanton, Atascosa Co., Sept. 23, 1916, *Palmer 10782* (MBG); Sutherland Springs, Wilson Co., July 10, 1938, *Parks & Ammerman 62* (MBG); Del Rio, Val Verde Co., April 18, 1935, *Parks & Cory 12290* (SMT); south-central Wilson Co., April 19, 1935, *Parks & Cory 12401*, and 11 mi. s. of Catarina, Dimmit Co., Oct. 7, 1935, *16946* (SMT); sandy plains, Laredo, July 24, 1889, *Pringle 2655* (MBG).

MEXICO:

NUEVO LEON: Sabinas Hidalgo, Sept. 16, 1936, *Kenoyer* (MBG); C. P. Diaz, April 18, 1900, *Trelease 66* (MBG).

COAHUILA: between Hipolito and Sacramento along a dry creek bed in El Desierto de la Payla, Ramos Arizpe, June 15, 1936, *Wynn & Mueller 83*, and San Lazaro, near n. entrance of El Puerto de San Lazaro, Castanos, June 16, 1936, *120* (MBG).

3a. *Othake texanum* var. *macrolepis* (Rydb.) Ammerman, comb. nov.

O. macrolepis Rydb. in Bull. Torr. Bot. Club. **37**:332. 1910, and in N. Am. Fl. **34**:60. 1914, Fl. Rocky Mts. & Adj. Plains, 944. 1917, and Fl. Prairies & Plains Cent. N. Am. 854. 1932.

Polypteris macrolepis (Rydb.) Cory in *Rhodora* **38**:408. 1936.

Stem herbaceous, 1.5–4.0 dm. high; leaves linear-lanceolate to lanceolate; peduncles glandular-pubescent; achenes about 6 mm. long, canescent-pubescent; pappus-scales about 8, ovate-lanceolate, 6–8 mm. long, attenuate-acuminate; in other characters as the species.

Distribution: Wyoming and Colorado.

WYOMING: sandy knoll, T. 38N., R. 67W., n. e. Converse Co., June 25, 1936, *Ownbey 1051* (MBG, NYB).

COLORADO: Rule Creek, Bent Co., Aug. 17, 1909, *Osterhout 4097* TYPE, and June 10, 1910, *4314* (NYB).

4. *Othake Lindenii* (Gray) Bush in Trans. Acad. Sci. St. Louis **14**:173. 1904; Rydb. in N. Am. Fl. **34**:60. 1914.

Palafoxia Lindenii Gray, Smiths. Contrib. to Knowledge (Pl. Wright. Pt. 1) **3**:120. 1852; Walp. Ann. Bot. Syst. **5**:161. 1858.

Polypteris Lindenii Gray in Proc. Am. Acad. **19**:30. 1883.

A simple or sparingly branched herbaceous annual; stem 4–7 dm. high, strigillose throughout, shallowly furrowed, gray-brown; leaves petiolate, oblong-

lanceolate to elliptic, 4–6 cm. long, 5–7 mm. broad, obtuse, narrowed at the base, puberulent on both surfaces, thick, obscurely 3-nerved, petioles 0.7–1.0 cm. long, expanded at the base; peduncles rather stout, long, densely glandular; heads few, about 1.7 cm. high; involucre bracts 11–15, linear to oblanceolate, about 9 mm. long, acute to obtuse, somewhat fimbriate at the apex, strigose, glandular; florets 18–25 in a head; corolla-lobes linear, 4 mm. long, acute to obtuse, somewhat pubescent at the tips; throat cylindric-campanulate, 1.5 mm. long, glabrous; tube slender, expanded at the base, 4.5 mm. long, not pubescent, finely glandular; achenes about 7 mm. long, glabrous or nearly so; pappus-scales 9–10, ovate-lanceolate, 4–6 mm. long, obtuse, the callose rib glabrous and extending to the tip of the scale, the hyaline margin erose near the apex.

Distribution: southern Mexico.

MEXICO:

VERA CRUZ: near the shore, n. of Vera Cruz, Jan. 24, 1906, *Greenman* 95 (G); Gulf Coast, Sept. 1912, *Purpus* 6025 (MBG, G); Antigua, June, 1838, *Linden*, fragments of TYPE, and Vera Cruz, sand-hills near the sea, 1840, *Galeotti* 2627 (G).

5. *Othake Reverchonii* Bush in Trans. Acad. Sci. St. Louis 14:180. 1904.

Polypteris Reverchonii (Bush) Small, Fl. Southeast. U. S., ed. 2, 1373. 1913.

A slender, herbaceous annual; stem 3–5 dm. high, simple below, with a few spreading branches above, terete, strigose, eglandular or minutely glandular in the upper parts, furrowed; leaves petiolate, linear to lanceolate-linear, 4–6 cm. long, 2–6 mm. broad, acute, narrowed at the base, slightly scabrous on both surfaces, 1-nerved, rarely 3-nerved, petioles 5–7 mm. long; peduncles long, slender, divaricate, strigose, eglandular or finely glandular; heads few, 1.0–1.4 cm. high; involucre bracts 7–9, oblanceolate, about 9 mm. long, acute or obtuse and somewhat fimbriate at the apex; ray-florets 4–6, the limb deeply 3-lobed, about 8 mm. long, the tube slender, densely glandular-pubescent, about 5 mm. long; disc-florets 5–6, the corolla-lobes 3 mm. long, linear; the cylindraceous, glabrous throat 2 mm. long; the tube 4 mm. long, slender, finely glandular-pubescent; achenes 5 mm. long, pubescent; pappus-scales 8, those of the ray-florets obovate, about 0.6 mm. long, obtuse, erose, those of the disc florets lanceolate, about 5 mm. long, lacerate-erose near the apex, the midrib dorsally pubescent.

Distribution: eastern Texas.

TEXAS: 2 mi. s. of Grapeland, Houston Co., Oct. 12, 1937, *Cory* 26155 (MBG); Cherokee, Oct. 31, 1884, *Joor* (MBG); dry sands, Big Sandy, Upshur Co., Sept. 27, 1926, *Palmer* 31756, and Sept. 16, 1902, *Reverchon* 3289 TYPE (MBG).

6. *Othake sphacelatum* (Nutt. ex Torr.) Rydb. in Bull. Torr. Bot. Club 37:331. 1910, and Fl. Rocky Mts. and Adj. Plains, 944. 1917; Britt. & Brown, Illust. Fl. 3:507, fig. 4534. 1913; Wootton & Standley in Contrib. U. S. Nat. Herb. 19:722. 1915.

Stevia sphacelata Nutt. ex Torr. in Ann. Lyc. N. Y. 2:214. 1828.¹⁷

¹⁷ A specimen of *O. callosum* in the Herbarium of the Academy of Natural Sciences of Philadelphia, bearing the label *Stevia sphacelata* in Nuttall's handwriting, indicates that Nuttall probably intended to give the latter name to his *S. callosa*. The confused history of the name *S. sphacelata* is set forth by Rydberg in the Bull. Torr. Bot. Club 37:331. 1910.

Palafoxia Hookeriana β . *subradiata* Torr. & Gray, Fl. N. Am. 2:368. 1842; Gray in Smiths. Contrib. to Knowledge (Pl. Wright., Pt. 1) 3:120. 1852.

Polypteris Hookeriana Gray in Proc. Am. Acad. 19:30. 1884, in part, and Syn. Fl. N. Am. 1²:337. 1884, and ed. 2, 1886, in part; Coulter in Contrib. U. S. Nat. Herb. 2:230. 1892, in part; Small, Fl. Southeast. U. S., 1287, ed. 1, 1903, and ed. 2, 1913; Coulter & Nelson, Man. Cent. Rocky Mts. 555. 1909.

Palafoxia Hookeriana Hooker in Curtis's Bot. Mag. 91:t. 5549. 1865, not Torr. & Gray, Fl. N. Am. 2:368. 1842.

O. Hookerianum (Torr. & Gray) Bush in Trans. Acad. Sci. St. Louis 14:177. 1904, excluding synonymy.

An herbaceous annual; stem 3–6 dm. high, somewhat geniculate, branched throughout with ascending branches, terete, strigose, shallowly furrowed; leaves petiolate, linear-lanceolate to lanceolate, 4–6 cm. long, 0.5–1.5 cm. wide, acute to obtuse, strigose on both surfaces, 3-nerved, petioles 0.6–1.0 cm. long; peduncles rather stout, densely glandular; heads few, 1.6–2.2 cm. high; involucre bracts 9–11, oblanceolate, about 1 cm. long, acute, strigose, glandular, the outer series often herbaceous throughout, the inner bracts with sphacelate, reddish tips; ray-florets 5–8, the limb 1.0–1.5 cm. long, deeply 3-cleft, the lobes rounded, the slender, glandular-pubescent tube 6 mm. long; disc-florets 15–20, the corolla-lobes linear, about 4 mm. long, the throat cylindraceous, 2 mm. long, glabrous, the tube filiform and dilated at the base, 8 mm. long, puberulent, eglandular; achenes 7–8 mm. long, pubescent; pappus-scales about 8, those of the ray-florets obovate, 1 mm. long or less, obtuse, erose, those of the disc-florets lanceolate, 8–9 mm. long, slightly exceeding the tube, attenuate, the midrib dorsally pubescent or glabrous.

Distribution: southwestern Kansas and Colorado southward to northern Mexico.

WITHOUT DEFINITE LOCALITY: *James* (NYB), TYPE.

KANSAS: Arkalon, Oct. 23, 1892, *Carleton* (NYB); sand hills, Hamilton Co., Aug. 3, 1895, *Hitchcock* 288 (MBG, NYB); Garden City, Aug. 14, 1896, *Letterman* (MBG); Arkalon, Aug. 17, 1890, *Smyth* 783 (MBG); Syracuse, Hamilton Co., July 4, 1893, *Thompson* 76 (NYB).

OKLAHOMA: Frederick, July 6, 1903, *Duncan* 29 (MBG); sand-dunes, s. e. Beckham Co., Oct. 18, 1936, *Eskew* 1524 (MBG); Red River bottoms, 10 mi. n. of Quanah, Texas, Aug. 21, 1921, *Ferris* & *Duncan* 3365 (NYB); sandy soil near roadside, 3 mi. n. of Alva, Woods Co., July 19, 1934, *Goodman* 2175, and banks of the North Fork of the Red River, near Sayre, Beckham Co., Sept. 12, 1934, 2354 (MBG); sand dunes along small tributary of North Canadian River, near Beaver, Beaver Co., July 24, 1933, *Palmer* 41895 (MBG); in sandy soil by Wolf Creek, near Shattuck, Ellis Co., Oct. 11, 1913, *Stevens* 2908 (MBG); sandy soil by river, 1 mi. n. of Sayre, Beckham Co., Aug. 8, 1927, *Stratton* 331, and 2 mi. n. of Beaver City, Beaver Co., Aug. 20, 1927, 411 (MBG); sand hills, Cimarron R., July 12, 1899, *White* 250 (MBG, NYB); Woodward Co., July 12, and July 13, 1900, *White* (MBG).

TEXAS: in sand desert on State Highway 51, near Crane, Crane Co., July 19, 1938, *Cutak* 6 (MBG); sandy ground near the Canadian River, Hemphill Co., Aug. 10, 1900, *Eggert* (MBG); grassy sand hills, 2 mi. s. of Muleshoe, Bailey Co., Aug. 24, 1921, *Ferris*

♂ *Duncan 3411* (MBG, NYB); 1 mi. n. of bridge over Canadian R., Amarillo-Dalbart Rd., Oldham Co., Aug. 27, 1921, *Ferris & Duncan 3501* (MBG); along railway, Amarillo, Potter Co., July 13, 1917, *Potter 12543* (MBG); sandy open ground, along river, Canadian, Hemphill Co., June 17, 1918, *Palmer 14100* (MBG); sands, Tascosa, June 24, 1902, *Reverchon 3219* (MBG).

COLORADO: Fort Collins, Sept. 25, 1894, *Baker* (NYB); Fort Morgan, Sept. 4, 1918, *Hapeman* (MBG).

NEW MEXICO: 35 mi. w. of Roswell, Chaves Co., Aug., 1900, *Earle & Earle 381* (MBG, NYB); sand plain n. of Magdalena, Datil Forest, Socorro Co., Oct. 2, 1919, *Eggleston 16193* (MBG); sandy soil, Jemez Springs, Aug. 24, 1931, *Nelson 11680* (MBG); Carlsbad, Oct. 3, 1902, *Tracy 8163* (MBG); Mesilla, Dona Ana Co., June 17, 1897, *Wooton 28* (MBG, NYB); Mesilla Valley, Dona Ana Co., Oct. 10, 1907, *Wooton* (MBG).

MEXICO:

CHIHUAHUA: sand hills near Paso del Norte, Sept. 20, 1886, *Pringle 761* (MBG).

7. Othake Hookerianum (Torr. & Gray) Bush in Trans. Acad. Sci. St. Louis **14**:179. 1904, as to name only; Rydb. in N. Am. Fl. **34**¹:61. 1914.

Palafoxia Texana Hook. Ic. Pl. **2**:pl. 148. 1837, not DC. Prodr. **5**:125. 1836.

Palafoxia Hookeriana Torr. & Gray, Fl. N. Am. **2**:368. 1842, not Hooker in Curtis's Bot. Mag. **91**:t. 5549. 1864; Walp. Rep. Bot. Syst. Suppl. **1**:949. 1843.

Polypteris Hookeriana (Torr. & Gray) Gray in Proc. Am. Acad. **19**:30. 1883, in part, and Syn. Fl. N. Am. **1**²:337. 1884, and ed. 2, 1886, in part; Coulter in Contrib. U. S. Nat. Herb. **2**:230. 1892, in part; Coulter & Nelson, New Man. Bot. Cent. Rocky Mts. 555. 1909.

Polypteris maxima Small, Fl. Southeast. U. S. 1288. ed. 1, 1903, and ed. 2, 1913.

O. maximum (Small) Bush in Trans. Acad. Sci. St. Louis **14**:179. 1904.

A stout annual; stems 4–10 dm. high, usually unbranched below the inflorescence, erect, terete, densely glandular-pubescent and usually viscid throughout, furrowed; leaves petiolate, lanceolate, 6–10 cm. long, 0.8–1.4 cm. wide, acute or acuminate, narrowed at the base, roughly scabrous on both surfaces, 3-nerved, petioles about 1.5 cm. long, densely glandular; peduncles long, stout, viscid; heads few, 2.0–2.5 cm. high; involucre bracts 15–17, oblanceolate, about 1.5 cm. long, acute, densely glandular-pubescent, the outer series usually herbaceous throughout, the inner bracts with a sphacelate, reddish tip; ray-florets 8–12, the limb deeply 3-cleft, about 1.5 cm. long, the lobes rounded, the tube slender, about 7 mm. long, glandular-pubescent; disc-florets 50–60, the lobes of the corolla linear, about 4 mm. long, the tips pubescent and somewhat glandular without, the cylindraceous, glabrous throat 2 mm. long, the slender tube about 6.5 mm. long, dilated at the base and finely glandular-pubescent; achenes 7 mm. long, pubescent; pappus-scales 8, those of the ray-florets obovate, subequal, 1 mm. or less long, acute or obtuse, the margin erose, those of the disc-florets lanceolate, subequal, 7–8 mm. long, slightly exceeding the tube, acuminate, the midrib dorsally pubescent.

Distribution: southeastern Texas.

TEXAS: Sutherland Springs, Wilson Co., July 18, 1938, and Nov. 1938, *Bremer*, and July 10, 1938, *Parks, Bremer & Ammerman* (MBG); Milano, Oct. 28, 1918, *Joor* (MBG);

Industry, Aug. 1844, *Lindheimer* (MBG); without definite locality, ex. Herb. Chapman, *Lindheimer* (NYB); sand dunes, Flour Bluff, Nueces Co., Sept. 9, 1939, *Parks* (MBG).

DOUBTFUL SPECIES

Othake tenuifolium Raf. New Fl. Am. 4:74. 1836. This plant is described by Rafinesque as being similar to *O. callosum* but having very large leaves; it could not be identified with any available specimens.

POLYPTERIS

Polypteris Nutt. Gen. N. Am. Pl. 2:139. 1818, not Less. in *Linnaea* 6:518. 1831, nor DC. Prodr. 5:659. 1836; Ell. Sketch Bot. S. Car. & Ga. 2:313. 1824; Gray in Proc. Am. Acad. 19:30. 1883, in part, and Syn. Fl. N. Am. 1²:74, 337. 1884, and ed. 2, 1886, in part; Chapman, Fl. South. U. S., ed. 3, 261. 1897, in part; Small, Fl. Southeast. U. S. 1287. ed. 1, 1903, and ed. 2, 1913, in part; Bush in Trans. Acad. Sci. St. Louis 14:172. 1904; Gray, Manual, ed. 7, 843. 1908, in part; Coulter & Nelson, New Man. Bot. Cent. Rocky Mts. 555. 1909, in part; Rydb. in N. Am. Fl. 34¹:61. 1914; Small, Man. Southeast. Fl. 1462. 1933, in part.

Paleolaria Cass. in Bull. Soc. Phil. 198. 1816, in part; Less. Syn. Comp. 155. 1832, in part.

Palafoxia DC. Prodr. 5:124. 1836, in part, not Lag. Gen. et Sp. Nov. 26. 1816, in part; Benth. & Hook. Gen. Pl. 2:405. 1873.

Lomaxeta Raf. New Fl. Am. 4:72. 1836.

Herbaceous, caulescent perennials with long, slender, fibrous roots. Stems several from a common base, strigillose, eglandular. Leaves alternate or the lower opposite, entire, thick, 1-3-nerved. Heads discoid, in a terminal, corymbiform cluster. Involucre turbinate, the bracts 2-3-seriate, membranaceous, not enfolding the marginal achenes, several of the outer series short and spreading or reflexed. Receptacle flat, naked, pitted, the surface uneven because of irregular aggregations of tissue around the base of the achenes. Corollas regular, deeply 5-lobed, the campanulate throat shorter than the spreading lobes or the slender tube. Stamen-tube completely exserted, the anthers obtuse or rounded at the base. Style-branches linear, obtuse or somewhat acute, exserted from the stamen-tube, spreading or recurved, hispidulous. Achenes 4-5-angled, obpyramidal, pubescent. Pappus of about 10 scarios, subequal scales with a midrib extending to the tip, the squamellae of the marginal achenes not reduced.

Type species: *Polypteris integrifolia* Nutt. Gen. N. Am. Pl. 2:139. 1818.

1. **Polypteris integrifolia** Nutt. Gen. N. Am. Pl. 2:139. 1818, not DC. Prodr. 5:659. 1836; Ell. Sketch Bot. S. Car. & Ga. 2:314. 1824; Chapman, West. Jour. Med. & Surg. 471. 1845; Gray, Syn. Fl. N. Am. 1²:337. 1884, and ed. 2, 1886; Chapman, Fl. South. U. S. ed. 3, 261. 1897; Small, Fl. Southeast.

U. S., ed. 1, 1287. 1903, and ed. 2, 1913; Rydb. in N. Am. Fl. 34¹:62. 1914; Small, Man. Southeast. Fl. 1462. 1933.

Hymenopappus integrifolius Spreng. Syst. 3:449. 1826.

Paleolaria fastigiata Less. Syn. Comp. 156. 1832.

Palafoxia fastigiata DC. Prodr. 5:125. 1836; Dietrich, Syn. Pl. 1345. 1847.

Lomaxeta verrucosa Raf. New Fl. Am. 4:72. 1836.

Palafoxia integrifolia Torr. & Gray, Fl. N. Am. 2:368. 1842; Walp. Rep. Bot. Syst. Suppl. 1:949. 1843; Benth. & Hook. Gen. Pl. 2:405. 1873; Hoffm. in Engler & Prantl, Die Nat. Pflanzenfam. IV, Abt. 5, p. 261. 1891.

An herbaceous perennial, woody at the base; stem 9–12 dm. high, sparingly branched below the inflorescence, erect, terete, strigillose throughout or nearly glabrous below, furrowed, brown; leaves petiolate, linear to oblong-lanceolate, 3–8 cm. long, 0.2–1.0 cm. wide, obtuse to somewhat acute, narrowed at the base, scabrous on both surfaces, dark green, the tuberculate hair-bases often white and conspicuous, petioles 3–8 mm. long; peduncles slender or slightly enlarged below the heads, strigose; heads numerous, 1.5–2.0 cm. long; involucre bracts about 15, oblong to oblong-spatulate, usually about 9 mm. long, membranaceous, truncate, rounded or obtuse, somewhat erose at the apex, flat, thin, finely scabrous or glabrous, stramineous, the short, reflexed, outer bracts 2.5 mm. long and somewhat herbaceous; florets 17–20 in a head, white or flesh-colored; corolla-lobes linear, 4 mm. long, acutish, the tips thickened and pubescent without; throat campanulate, 2 mm. long, glabrous; tube very slender, abruptly dilated at the base, 6 mm. long, pubescent; style-branches exerted about half their length from the stamen-tube; achenes 5–6 mm. long, puberulent; pappus-scales 9–11, lanceolate, subequal, 5–7 mm. long, exceeding the corolla-tube, acuminate, the hyaline margin erose or somewhat lacerate, the callose midrib dorsally pubescent.

Distribution: southern Georgia and Florida.

GEORGIA: without definite locality, *Baldwin* (ANSP), TYPE.

FLORIDA: Quincy, *Chapman* (ANSP); dry pine-barrens, near Apalachicola, Oct. 15, 1890, *ex Herb. Chapman 791a* (MBG); dry pine-barrens, Aspalaga, Oct. 1897, *ex Herb. Chapman 791b* (MBG); dry pine-barrens, near Jacksonville, Oct., *Curtiss 1507* (ANSP, MBG); near Jacksonville, Oct. 11, 1893, *Curtiss 4494* (MBG); pine-barrens, Indian River region, Brevard Co., Nov. 28, 1902, *Fredholm 5623* (MBG); Tampa, Oct. 1877, *Garber* (ANSP); in the vicinity of Eustis. June and July, 1894, *Hitchcock* (MBG); Miami, March, 1917, *Meredith* (ANSP); high pine-land, in the vicinity of Eustis, Lake Co., July 1–15, 1894, *Nash 1191* (MBG); dry pine woods, Polk Co., May 20, 1894, *Oblinger 349* (MBG); dry pine-lands, St. Leo, King Lake, Oct. 10, 1926, *O'Neill 1922* (MBG); Biscayne Bay, 1874, *Palmer* (MBG); Palatka, Dec. 5, 1871, *ex Herb. Porter* (ANSP); Miami, *Small & Carter* (ANSP); between Coconut Grove and Cutler, Dade Co., Nov. 1903, *Small & Carter 1231* (ANSP); Eustis, Oct. 8, 1896, *Webber 532* (MBG); St. Petersburg, Aug. 1894, *Williamson* (ANSP).

EXCLUDED SPECIES

Polypteris brasiliensis Less. in Linnaea 6:518. 1831 (= *Gaillardia lanceolata* Michx).

PALAFOXIA

Palafoxia Lag. Elench. Pl. Hort. Matr. 26. 1816, and Gen. et Sp. Nov. 26. 1816; Spreng. Syst. 3:449. 1826; DC. Prodr. 5:124. 1836, in part; Benth. & Hook. Gen. Pl. 2:405. 1873, in part; Gray, Geol. Surv. Calif. Bot. 1:387. 1876, in part, and in Proc. Am. Acad. Sci. 19:30. 1883; Baillon, Hist. des Plantes 8:249. 1886, in part; Gray, Syn. Fl. N. Am. 1²:74, 338. 1884, and ed. 2, 1886; Hoffm. in Engl. & Prantl, Die Nat. Pflanzenfam. IV, Abt. 5, p. 261. 1891, in part; Small, Fl. Southeast. U. S. 1288. 1903, and ed. 2, 1913; Jepson, Man. Fl. Pl. Calif. 1127. 1925; Small, Man. Southeast. Fl. 1463. 1933; Munz, Man. South. Calif. Bot. 563. 1935.

Paleolaria Cass. in Bull. Soc. Phil. 198. 1816, and in Dict. Sci. Nat. 1, Suppl. 59. 1816, and 38:256. 1825.

Herbaceous, branching annuals, often becoming woody below and perennial. Stem usually one from a tap-root, strigose to hispid, eglandular to densely glandular-pubescent. Leaves alternate or the lower opposite, entire, thick, 1-3-nerved. Heads discoid, in cymose or corymbiform clusters terminating the branches. Involucre oblong or turbinate, the bracts in 2-3 series, subequal, entirely herbaceous, rarely membranaceous. Receptacle flat, naked, foveolate. Corollas regular, 5-lobed, the cylindraceous throat much longer than the corolla-lobes and short tube. Stamen-tube partly exerted from the throat, the anthers obtuse or rounded at the base. Style-branches filiform, spreading or recurved, hispidulous. Achenes quadrangular, linear to obpyramidal, pubescent. Pappus-scales several to 10, unequal, hyaline and scarious with a stout callose midrib, the scales of the marginal achenes often reduced.

Type species: **Palafoxia linearis** Lag. Elench. Pl. Hort. Matr. 26. 1816.

KEY TO THE SUBGENERA

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|--|------------------------|
| A. Involucral bracts entirely herbaceous, green, somewhat keeled, closely enfolding the mature marginal achenes; pappus-scales longer than the corolla-tube..... | EUPALAFOXIA. Sp. 1 |
| AA. Involucral bracts membranaceous, purplish, flat, not enfolding the outer achenes; pappus-scales shorter than the corolla-tube..... | PSEUDOPALAFOXIA. Sp. 2 |

KEY TO THE SPECIES AND VARIETIES

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|--|--|
| A. Involucral bracts herbaceous; pappus-scales longer than the corolla-tube. | |
| B. Pappus-scales of the inner florets of the head acerose, equalling or exceeding the throat; plants erect. | |
| C. Peduncles glandular-pubescent; leaves 2-6 mm. broad; florets about 15 in a head..... | 1. <i>P. LINEARIS</i> |
| CC. Peduncles almost eglandular; leaves 8-11 mm. broad; florets about 25 in a head..... | 1a. <i>P. LINEARIS</i> var. <i>GIGANTEA</i> |
| BB. Pappus-scales of the inner florets of the head obtuse or emarginate, shorter than the throat; plants somewhat decumbent..... | 1b. <i>P. LINEARIS</i> var. <i>LEUCOPHYLLA</i> |
| AA. Involucral bracts membranaceous; pappus-scales shorter than the corolla-tube..... | 2. <i>P. FRAYI</i> |

1. *Palafoxia linearis* (Cav.) Lag. Elench. Pl. Hort. Matr. 26. 1816, and Gen. et. Sp. Nov. 26. 1816; Hook. in Curtis's Bot. Mag. 47:t. 2132. 1820; Spreng. Syst. Veg. 3:449. 1826; DC. Prodr. 5:124. 1836; Dietrich, Syn. Pl. 1345. 1847; Gray, Geol. Surv. Calif. Bot. 1:338. 1876, and Syn. Fl. N. Am. 1²:338. 1884, and ed. 2, 1886; Rydb. in N. Am. Fl. 34¹:62. 1914; Jepson, Man. Fl. Pl. Calif. 1127, fig. 992. 1925; Tidestrom in Contrib. U. S. Nat. Herb. 25:591. 1925; Munz, Man. South. Calif. Bot. 563. 1935.

Ageratum lineare Cav. Ic. 3:3, t. 205. 1794.

Stevia linearis Cav. Praelect. n. 464, and Ic. 4:32. 1797; Willd. Sp. Pl. 1774. 1804.

Stevia lavendulaefolia Schlecht. in Suppl. to Willd. Enum. Pl. 57. 1813; DC. Prodr. 5:125. 1836, in synonymy.

Paleolaria carnea Cass. in Bull. Soc. Phil. 47. 1818, and in Dict. Sci. Nat. 38:256. 1825; Less. Syn. Comp. 155. 1832.

An herbaceous annual, occasionally suffrutescent and perennial; stem 1–7 dm. high, divaricately branched throughout, ascending, terete, furrowed, scabrous to roughly hispid, the upper parts glandular; leaves petiolate, linear to linear-lanceolate, 4–6 cm. long, 2–6 mm. wide, obtuse, entire, attenuated at the base, canescent-scabrous on both sides, thick, 1-nerved, often indistinctly 3-nerved, petioles 0.3–1.0 cm. long; peduncles long, slightly scabrous, densely glandular; heads in cymose or corymbiform clusters, 2–3 cm. high; involucre oblong to obconic, the bracts 7–13, linear-oblong, 1.0–1.5 cm. long, herbaceous throughout or those of the inner series with hyaline margins, acute to obtuse, scabrous, finely glandular, somewhat keeled, slightly saccate at the base, closely enfolding the marginal achenes; florets 10–18 in a head; corolla-lobes 1.5 mm. long, obtuse, the tips pubescent without; throat cylindraceous, about 5 mm. long, glabrous; tube slender, 2.5–3.5 mm. long, scarcely dilated at the base, glabrous to glandular-pubescent; achenes 1.0–1.5 cm. long, linear, attenuated downward; pappus-scales 3–8, unequal, the inner florets having either 4 long scales exceeding the throat, 0.7–1.0 cm. long, lanceolate, with a stiff, acerose midrib, alternating with 4 small, obtuse scales with included ribs, or 8 unequal scales, the marginal florets having 3–8 scales like those of the inner achenes or reduced to minute callosities with narrow, hyaline margins.

Distribution: Arizona to southern California.

ARIZONA: Yuma, *Beard 1911* (MBG); 20 mi. above Pierce's Ferry, April 19, 1894, *Jones 5081* (MBG); 11 mi. e. of Gila Bend, April 10, 1932, *Jones 29466* (MBG); sand desert on Ariz.-Nev. line, along U. S. Highway 91, Mohave-Clark Counties, April 4, 1934, *Maguire, Maguire & Maguire 5067* (MBG); in the Fortuna Range, Yuma, Feb. 26, 1930, *Nelson 11143a* (MBG); Williams Fork of the Colorado River, March 11, 1876, *Palmer 10253* (MBG).

NEVADA: sandy, stony washes, Virgin River, May 5, 1902, *Goodding 709* (MBG); desert 1 mi. w. of Riverside, Clark Co., May 19, 1933, *Maguire & Blood 4505* (MBG).

CALIFORNIA: old beach, Colorado Desert, San Diego Co., March 24, 1903, *Abrams 3147* (MBG); near Yaqui Wells, Colorado Desert, San Diego Co., April 12, 1913, *East-*

wood 2676 (MBG); White Water Desert, Nov. 11, 1890, *Engelmann* (MBG); Palm Springs, March, 1927, *Epling* (MBG); alluvial fan, Opher mine, Mohave Desert, Slate Mts., April 18, 1930, *Epling, Ellison & Anderson* (MBG); sand flat, Thousand Palms Canyon, Coachella Valley, Riverside Co., March 13, 1932, *Fosberg 8093* (MBG); wash, w. end of Sheep Hole Mts., San Bernardino Co., April 24, 1932, *Fosberg 8172* (MBG); western borders of the Colorado Desert, Coyote Canyon, Lower Sonoran Zone, April, 1902, *Hall 2768* (MBG); Palm Springs, Apr. 1926, *Haupt* (MBG); sandy wash, Deep Canyon, Coachella Valley, Riverside Co., March 14, 1932, *Munz 11975* (MBG); sandy wash, 5 mi. n. w. of Dixieland, Imperial Co., April 4, 1932, *Munz & Hitchcock 12109* (MBG); Indian Springs, Colorado Desert, June 24, 1888, *Orcutt 1500* (MBG); s. w. part of the Colorado Desert, San Diego Co., Nov. 1889, *Orcutt* (MBG); Carris Creek, Colorado Desert, April 25, 1890, *ex Orcutt Herb. 2241* (MBG); Indio, Colorado Desert, April 24, 1891, *ex Orcutt Herb.* (MBG); Whitewater, Riverside Co., March, 1882, *Parish 4*, and June 14, 1894, *3109* (MBG); Palm Springs, desert base of San Jacinto Mt., April 4-13, 1896, *Parish 4121* (MBG); desert wash, 15 mi. w. of Indio, L. A. Aqueduct Rd., Colorado Desert, Riverside Co., Jan. 1, 1936, *Rose 36003* (MBG).

1a. *Palafoxia linearis* var. *gigantea* Jones, Extracts from Contrib. West. Bot. 18:79. 1933; Munz, Man. South. Calif. Bot. 563, fig. 299. 1935.

Palafoxia linearis var. *arenicola* Nelson in Am. Jour. Bot. 23:265. 1936.

Stem erect, annual or perennial, 7-10 dm. high, glabrous or nearly so; leaves 6-8 cm. long, 8-11 mm. broad, distinctly 3-nerved; peduncles strigose and almost eglandular; heads large, 2.5-3.0 cm. high; involucre bracts about 24, strigose, eglandular; florets 25 or more; achenes about 1.5 cm. long; pappus-scales 8, unequal, 0.5-1.0 cm. long, the four long, acerose scales equalling or exceeding the throat, the four alternate scales very short, usually obtuse, with included midrib; in other characters as the species.

Distribution: California, in sand dunes west of Yuma, Arizona.

CALIFORNIA: w. of Yuma, Ariz., Sept. 24, *Jones 28599* TYPE, and Feb. 27, 1930, *Nelson 11161* (MBG); common in dunes e. of Holtville, Imperial Co., April 5, 1932, *Munz & Hitchcock 12131* (MBG).

1b. *Palafoxia linearis* var. *leucophylla* Johnston in Proc. Calif. Acad. Sci. IV. 12:1202. 1924

P. leucophylla Gray in Proc. Am. Acad. 8:291. 1870, and Geol. Surv. Calif. Bot. 1:388. 1876; Rydb. in N. Am. Fl. 34¹:63. 1914.

P. linearis Gray in Proc. Am. Acad. 19:31. 1883, not Lag. Gen. et Sp. Nov. 26. 1816.

P. arenaria Brandeg. in Proc. Calif. Acad. Sci. II. 2:178. 1889; Goldman in Contrib. U. S. Nat. Herb. 16:369. 1916.

A shrubby, somewhat decumbent, much-branched perennial; stem 4-10 dm. high, densely glandular-hispid and scabrous in the upper parts or throughout; heads 1.5-2.0 cm. long; pappus-scales about 8, unequal, not exceeding the throat, often no more than half the length of the throat, obtuse or emarginate, sometimes acute; in other characters as the species.

Distribution: Mexico, chiefly Baja California.

MEXICO:

COAHUILA: Torreon, Oct. 13-20, 1898, *Palmer 486* (MBG).

BAJA CALIFORNIA: sand dunes, San Nicholas Bay, May 16, 1921, *Johnston 3716* (MBG); sand dunes, Loreto, May 20, 1921, *Johnston 3776* (MBG); La Paz, Feb. 7, 1928, *Jones 24065* (MBG).

2. *Palafoxia Feayi* Gray in Proc. Am. Acad. 12:59. 1877; Chapman in Bot. Gaz. 3:6. 1878; Gray, Syn. Fl. N. Am. 1²:338. 1884, and ed. 2, 1886; Chapman, Fl. South. U. S., ed. 3, 261. 1897; Small, Fl. Southeast. U. S. 1288. 1903, and ed. 2, 1913; Rydb. in N. Am. Fl. 34¹:63. 1914; Small, Man. Southeast. Fl. 1463. 1933.

An herbaceous perennial, woody at the base; stem 4-10 dm. high, simple or branched, erect, terete, strigillose, furrowed; leaves petiolate, lanceolate-oblong to oblong-elliptic, 2.5-5.5 cm. long, 0.5-2.5 cm. broad, usually obtuse, slightly callose at the tip, rounded at the base, rather scabrous, the hair-bases often white and conspicuous, distinctly 3-nerved, petioles 2-6 mm. long; peduncles long and slender, strigillose, eglandular; heads numerous, in corymbiform clusters, 1.5-2.0 cm. high; involucre turbinate, the bracts 9-11, linear to oblong, 5-8 mm. long, membranaceous, thickened along the midvein, truncate or obtuse, often strigillose, purple-tipped or purplish throughout, several of the outer series shorter and reflexed, 2-4 mm. long; florets about 18 in a head; corolla-lobes 1.5-2.5 mm. long, obtuse, the tips thickened and pubescent without; throat cylindraceous, 4-5 mm. long, glabrous; achenes 6-8 mm. long, obpyramidal, sparingly pubescent; pappus-scales 8-10, usually obovate, subequal, 0.5-3.0 mm. long, obtuse, the scarious margin erose, the midrib dorsally pubescent and extending about two-thirds the length of the scale.

This species is intermediate between the genera *Polypteris* and *Palafoxia*, but it is placed in the latter group because of the floret characters. The nature of the involucre and the general habit of the plant, however, suggest a close alliance with *Polypteris*.

Distribution: Florida.

FLORIDA: Clear Water Harbor to Caxambas, *Chapman* (G); without definite locality, *Curtiss 102* (G); sandy soil, Indian River, Sept., *Curtiss 1507* (G); dry scrub near Seville, Volusia Co., July 17, 1900, *Curtiss 6688* (G, MBG); s. Florida, comm., Jan. 7, 1876, *Feay* (G), TYPE; dry pine-barrens, Indian River region, Brevard Co., Oct. 29, 1902, *Fredholm 5528a* (G); Caxambas Bay, Sept. 1878, *Garber 11870* (MBG); flat woods, Marco, Lee Co., July & Aug., 1900, *Hitchcock 139* (G, MBG); scrub land, Wekiwe Springs, Sept. 16, 1929, *O'Neill 5601* (MBG); dry, sandy soil, open scrub land, Kelsey City, Palm Beach Co., Nov. 25, 1920, *Randolph 157* (G); without definite locality, 1842-1849, *Rugel 60* (MBG); pine-lands about Arch Creek Prairie, Dade Co., July 3, 1915, *Small, Mosier & Small 6811* (G); Manatee, Sept. 12, 1899, *Tracy 6357* (MBG); Palma Sola, April 30, 1900, *Tracy 6932* (MBG).

LIST OF EXSICCATAE

The distribution numbers are indicated by *italics*, or, when the specimen is not numbered, by a dash. The numbers in parenthesis refer to the species in this study.

OTHACE

- Ammerman, Elizabeth. 7 (2); 8, 39 (1); 97 (3).
 Baker, Carl F. — (6).
 Barkley, Fred A. 1499 (3).
 Berlandier, Jean. 604, 2041 (3).
 Bremer, E. — (6).
 Bush, Benjamin F. 115, 204, 476, 1146 (1); 1599 (2); 3187, 3354, 4983, 14999, 15180, 15195, 15752, 15756, 15942 (1).
 Carleton, M. A. — (6).
 Clemens, Mrs. Joseph. — (6).
 Cory, V. L. 25366 (1); 26155 (5).
 Cutak, Ladislaus. — (6).
 Duncan, Mrs. F. T. 29 (6).
 Earle, F. S. & E. S. Earle. 381 (6).
 Eggert, Henry. — (1); — (2); — (6).
 Eggleston, W. W. 16193 (6).
 Emig, W. H. 43 (1).
 Eskew, C. T. 1502 (1); 1524 (6).
 Ferris, Roxana S. & Carl D. Duncan. 2915 (1); 3014 (3); 3365 (6); 3375 (3); 3411, 3501 (6).
 Galeotti, H. 2627 (4).
 Glatfelter, N. M. — (2).
 Goodman, George Jones. 2175, 2354 (6).
 Greenman, Jesse More. 95 (4).
 Griffiths, David. 6320 (3).
 Hall, Elihu. 356 (1).
 Hapeman, H. — (6).
 Heller, A. Arthur. 1562 (2a).
 Hitchcock, Albert S. 288 (6).
 James, E. P. — (6).
 ex Jermy Herb. 804 (1).
 Jones, Marcus E. 26398, 29467 (3).
 Joor, J. F. — (2); — (5); — (7).
 Kenoyer, Leslie A. — (3); 728 (2a).
 Letterman, George W. — (1); — (6).
 Linden, Jean-Jules. — (4).
 Lindheimer, Ferdinand. — (2); — (7); 955, 956 (1).
 Mackenzie, Kenneth K. — (1); 7 (3).
 Nelson, Aven. 11680 (6).
 Nuttall, Thomas. — (1).
 Orcutt, Charles Russell. 5548 (3).
 Osterhout, George E. 4097, 4314 (3a).
 Ownbey, Francis Marion. 1051 (3a).
 Palmer, Ernest J. 38 (2a); 4078, 4492, 4633, 4893, 6443a (1); 8575, 10732 (2); 10782 (3); 10898 (1); 12543 (6); 12856 (1); 14100 (6); 19067, 29531 (1); 31756 (5); 33012 (1); 41895 (6).
 Pammel, L. H. — (2).
 Parks, H. B. — (1); — (2a); — (7).
 Parks, H. B. & E. Ammerman. 62 (3).
 Parks, H. B., E. Bremer & E. Ammerman. — (7).
 Parks, H. B. & V. L. Cory. —, 12290, 12401 (3); 16941, 16942 (2a); 16946 (3); 20747, 20748 (1).
 Pringle, Cyrus Guernsey. 2655 (3); 6354 (2a).
 Purpus, C. A. 6025 (4).
 Reverchon, Jules. — (1); 1230 (2a); 2577 (2); 3219 (6); 3288 (1); 3289 (5); 3290 (2); 3655 (1); 3656 (2).
 Runyon, Robert. 209 (2a).
 Shepard, E. M. — (1).
 Smyth, H. B. 783 (6).
 Stevens, G. W. 2908 (6).
 Steyermark, Julian A. 14657 (1).
 Stratton, Robert A. 411 (6).
 Thompson, Charles H. 76 (6).
 Tracy, S. M. 8142 (1); 8163 (6).
 Trelease, William. — (2); 66 (3).
 Warner, Selden R. — (2).
 White, Mark. 250 (6).
 White, Paul. — (6).
 Wislizenus, Frederick W. — (1).
 Wooton, E. O. —, 28 (6).
 Wynd, F. Lyle & C. H. Mueller. 83, 120 (3).

POLYPTERIS

- Baldwyn. — (1).
 Chapman, A. W. — (1).
 ex Chapman Herb. 791a, 791b (1).
 Curtiss, A. H. 1507, 4494 (1).
 Fredholm, A. 5623 (1).
 Garber, A. P. — (1).
 Hitchcock, Albert S. — (1).
 Meredith, D. W. — (1).
 Nash, George Valentine. 1191 (1).
 Ohlinger, L. B. 340 (1).
 O'Neill, Hugh. 1922 (1).
 Palmer, Edward J. — (1).
 ex Porter Herb. — (1).
 Small, John Kunkel & J. J. Carter. —, 1231 (1).
 Webber, H. J. 532 (1).
 Williamson, C. S. — (1).

PALAFOXIA

- Abrams, LeRoy. 3147 (1).
 Beard, A. 1911 (1).
 Chapman, A. W. — (2).
 Curtiss, A. H. 102, 1507, 6688 (2).
 Eastwood, Alice. 2676 (1).
 Engelmann, George. — (1).
 Epling, Carl C. — (1).

Epling, Carl, Lincoln Ellison, & Harvey Anderson. — (1).
 Feay, W. (2).
 Fosberg, F. R. 8093, 8172 (1).
 Fredholm, A. 55284 (2).
 Garber, A. P. 11870 (2).
 Goodding, Leslie N. 709 (1).
 Hall, H. M. 2768 (1).
 Haupt, A. W. — (1).
 Hitchcock, Albert S. —, 139 (2).
 Johnston, Ivan M. 3716, 3776 (1b).
 Jones, Marcus E. 5081 (1); 24065 (1b), 28599 (1a); 29466 (1).
 Maguire, Bassett & H. L. Blood. 4505 (1).
 Maguire, Bassett, Ruth Maguire, & C.

B. Maguire. 5067 (1).
 Munz, Philip A. 11975 (1).
 Munz, Philip A. & Charles Leo Hitchcock. 12109 (1); 12131 (1a).
 Nelson, Aven. 111434 (1); 11161 (1a).
 O'Neill, Hugh. 5601 (2).
 Orcutt, Charles Russell. —, 1500 (1).
 ex Orcutt Herb. —, 2241 (1).
 Palmer, Ernest J. 468 (1b); 10253 (1).
 Parish, Samuel B. 4, 3109, 4121 (1).
 Randolph, Fannie R. 157 (2).
 Rose, Lewis S. 36003 (1).
 Rugel, F. 60 (2).
 Small, John Kunkel, S. A. Mosier, & Gertrude K. Small. 6811 (2).
 Tracy, S. M. 6357, 6932 (2).

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EXPLANATION OF PLATE

PLATE 10

Othake callosum

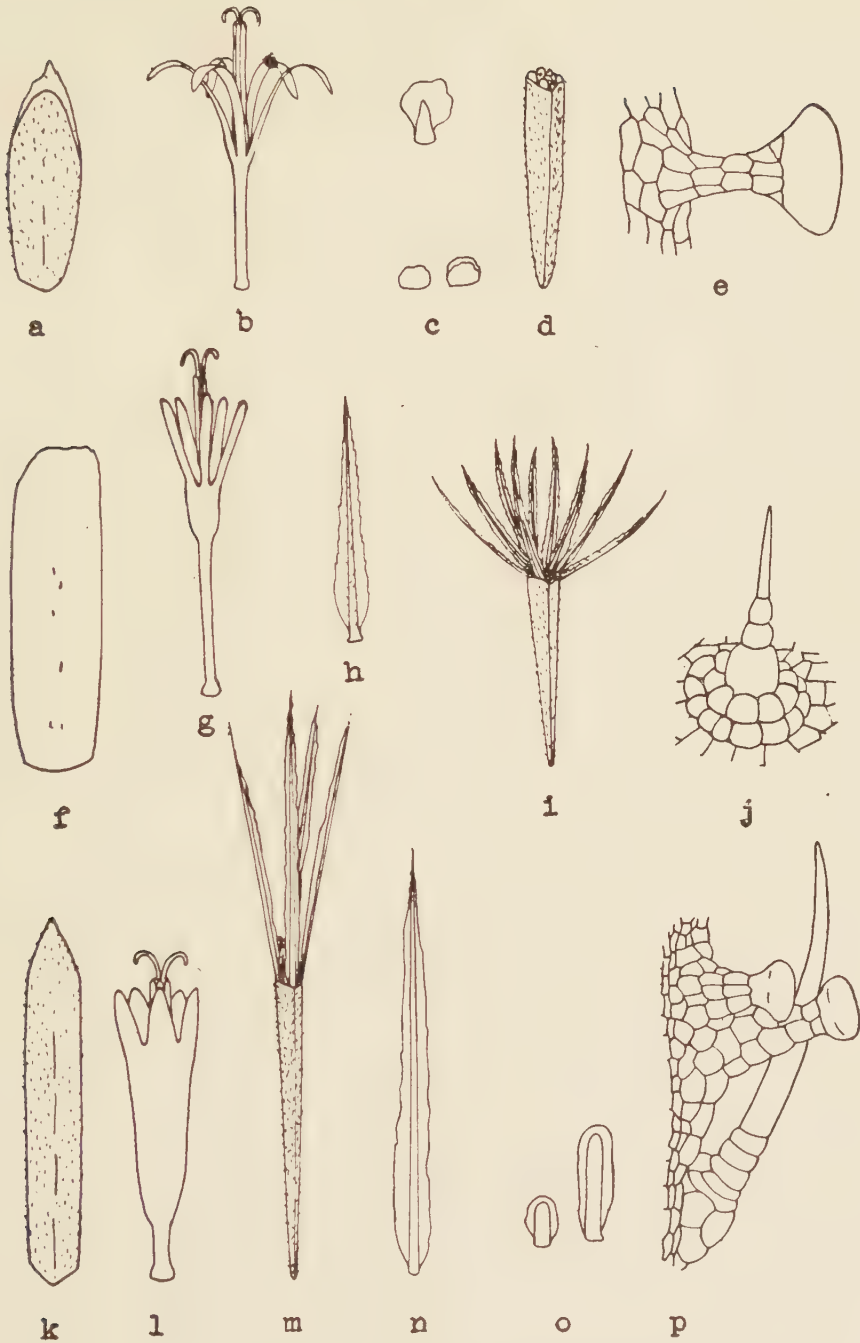
- a. involucre bract (x 5.7)
- b. corolla (x 5.7)
- c. pappus-scales (x 5.7)
- d. achene (x 9.5)
- e. glandular hair on peduncle, greatly magnified

Polypteris integrifolia

- f. involucre bract (x 4.75)
- g. corolla (x 2.8)
- h. pappus-scale (x 5.7)
- i. achene (x 4.75)
- j. tuberculate hair on leaf, greatly magnified

Palafoxia linearis

- k. involucre bract (x 4.75)
- l. corolla (x 5.7)
- m. achene (x 3.8)
- n. pappus-scale (x 5.7)
- o. pappus-scales of marginal achenes (x 7.6)
- p. hairs on peduncle, greatly magnified



AMMERMAN—PALAFOXIA AND ALLIES

EXPLANATION OF PLATE

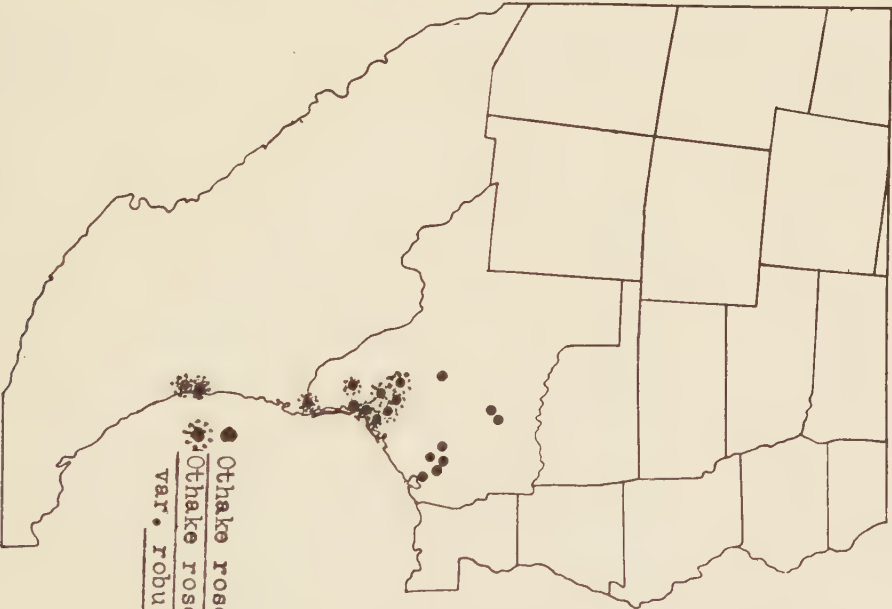
PLATE 11

Distribution of *Otbake callosum*, *O. roseum*, and *O. roseum* var. *robustum* as indicated by specimens in the Herbarium of the Missouri Botanical Garden.

AMMERMAN—PALAFOXIA AND ALLIES



Othake callosum



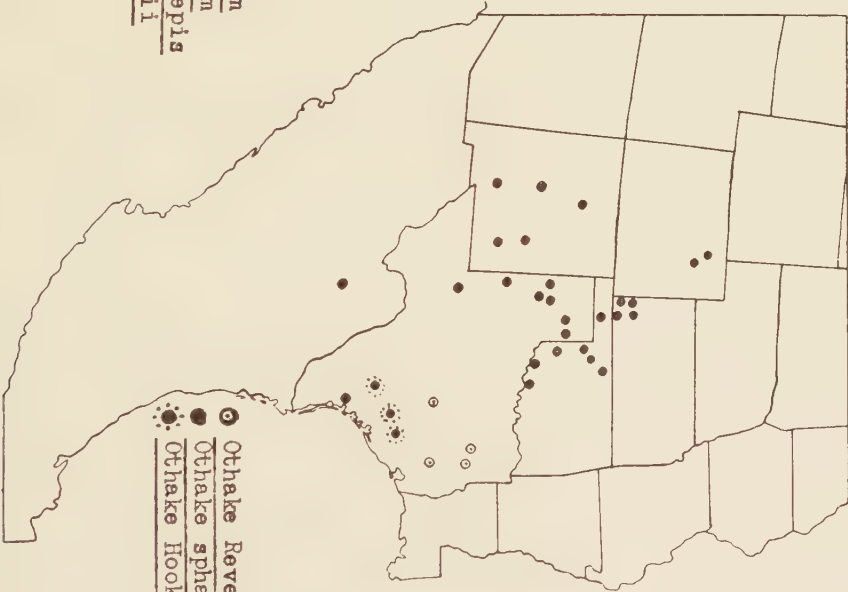
● Othake roseum
● Othake roseum
var. robustum

EXPLANATION OF PLATE

PLATE 12

Distribution of *Othake texanum*, *O. texanum* var. *macrolepis*, *O. Lindenii*, *O. Reverchonii*, *O. sphacelatum*, and *O. Hookerianum*, as indicated by specimens in the Herbarium of the Missouri Botanical Garden.

AMMERMAN—PALAFOXIA AND ALLIES



EXPLANATION OF PLATE

PLATE 13

Distribution of *Palafoxia linearis*, *P. linearis* var. *gigantea*, *P. linearis* var. *leucophylla*, *Polypteris integrifolia*, and *Palafoxia Feayi*, as indicated by specimens in the Herbarium of the Missouri Botanical Garden.



AMMERMAN—PALAFOXIA AND ALLIES

MONOGRAPH OF *PSILOSTROPHE*¹

CHARLES BIXLER HEISER, JR.

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INTRODUCTION AND HISTORY

In this paper there has been an attempt to clarify the confusion in the taxonomy of the genus *Psilostrophe*. It has necessitated a critical study of the morphology and of the geographical distribution of the several entities which comprise this interesting composite of southwestern North America. No novelties have been added in this treatment; rather it consists of a reduction in the number of species hitherto recognized.

Psilostrophe received its name from de Candolle² in the year 1838; the genus was based on specimens collected by Berlandier at San Luis Potosi, Mexico. Three years later Nuttall³ described a new genus, *Riddellia*, from a specimen collected by James on Long's Expedition, but no definite locality was recorded.⁴ *Riddellia* subsequently proved to be synonymous with *Psilostrophe*, but the name was used for the next half century before it lapsed into synonymy. Gray, who did much work on the genus, realized that his *Riddellia arachnoidea* was the same as de Candolle's *Psilostrophe gnaphalodes*.⁵ However, he later wrote:⁶ *Psilostrophe*, "a name which although a year or two earlier in publication [than *Riddellia*] we trust may remain disused, having been accompanied by an insufficient, and, in some important respects, erroneous character." Nevertheless, according to the International Rules of Botanical Nomenclature, the older name, *Psilostrophe*, should be used, although the genus may have been incorrectly described in some minor details. In 1891 it was restored as the valid generic name by Greene.⁷

Gray⁸ in his 'Synoptical Flora of North America' recognized three species and one variety of *Psilostrophe*. In the only paper approaching a monographic study of the genus,⁹ A. Nelson in 1903 included six species and two varieties, but this treatment is inadequate to meet present needs. Since that time the most important treatment of the genus is Rydberg's,¹⁰ where three new species are described, bringing the total number of species to ten, some of which are reduced in this monograph. Type material, or duplicates of types, of most of the species has been examined in this study.

¹ An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of master of science in the Henry Shaw School of Botany of Washington University.

² de Candolle, A. *Prodr.* 7:261. 1838.

³ Nuttall in *Trans. Am. Phil. Soc.* II. 7:371. 1841.

⁴ Gray in *Mem. Am. Acad.* II. 4:94. 1849.

⁵ Gray in *Smithson Contr. to Knowl.* 3:121. 1852.

⁶ Gray in *Proc. Am. Acad.* 7:358. 1868.

⁷ Greene, *Pittonia* 2:176. 1891.

⁸ Gray, *Syn. Fl. N. Am.* 1²:317. 1884, and ed. 2, 1886.

⁹ Nelson in *Proc. Biol. Soc. Wash.* 16:21. 1903.

¹⁰ Rydberg in *Britton, N. Am. Fl.* 34:6. 1914.

MORPHOLOGY

All the species of *Psilostrophe* arise from a ligneous tap root. The stems are generally somewhat striate, from almost glabrous in *P. sparsiflora* through all degrees of villosity to densely pannose in *P. Cooperi*. Gray¹¹ correctly describes the pubescence of the stem of *P. Cooperi* as "canescent with close and matted tomentum." The base of the plant, which is usually woody, is frequently more densely hairy than the upper part of the stem. The color of the stem varies, depending on the amount of pubescence, from green in *P. sparsiflora* and occasionally in *P. taetina*, to gray, and white in *P. Cooperi*. A slight twisting of the stem may show up somewhat in *P. taetina* var. *lanata* and is frequently very marked in *P. sparsiflora*.

The lower leaves vary in size up to 15 cm. in length and are usually less than half as broad. All measurements in this paper are from dried specimens. As a general rule, the leaves are less villous than the stems and involucres. In shape, there is a wide degree of variation from obovate to linear. Some of the leaves may be lobed in all of the species except in *P. Cooperi*. The lower leaves are quite frequently lacking on the herbarium specimens.

The upper leaves are alternate, generally entire, sessile, and smaller than the basal leaves. They are also usually less villous than the lower leaves and consequently greener. In shape, they vary from spatulate to linear. The leaves fail to offer much of taxonomic value in delimiting the species.

The involucre is cylindrical to campanulate and composed of one definite series of 4-12 linear-oblong or lanceolate connivent bracts, but which often appear connate because of the dense pubescence. There is an inner indefinite series of 1-7 smaller scarious bracts, and sometimes an outer calyculate bract is present.

The heads are on long peduncles up to 8.0 cm. in length in *P. Cooperi*; or they may be clustered on shorter peduncles; or almost sessile as in *P. gnaphalodes*. The length of the peduncles is of some taxonomic worth in distinguishing *P. gnaphalodes* and *P. villosa* from *P. taetina*, but this character by itself is of doubtful value because of intergradations.

The ligules, which are always some shade of yellow, become papery in age and persist on the achenes. There is great variation in the length of the ligules even among the same species. Nevertheless, the size often serves as a diagnostic character, for in *P. Bakeri* and *P. Cooperi* the ligules are from 8 to 14 or 16 mm. long, while in *P. villosa* they are only 3 to 5 mm. long. There is also a variation in the number of ligules present, 3-4 in most species, but from 4 to 8 in *P. Bakeri* and *P. Cooperi*. The ligules are 4-7-nerved, and the nerves unite in pairs within the lobes. Most of the species have shallowly 3-lobed ligules, rarely 4-5-lobed, but in *P. villosa* the lobes may extend half the length of the ligule. In some plants there may be found ligules with 3, 4, and 5 lobes on the same plant. The ligules, which are broader than long, are contracted at their base into a tube

¹¹ Gray, Syn. Fl. N. Am. 12:318. 1884, and ed. 2, 1886.

from which the style protrudes. The style-branches of the ray-flowers are elongated, subterete, and more or less acute at the apex.

The number of disk-flowers varies from as few as 5 to as many as 20, the larger number being found in *P. Cooperi* and *P. Bakeri*. The anthers are obtuse at the base, lanceolate, and acute at the tips, and the style branches are truncate-capitellate at the apex in contrast to those of the ray-flowers.

The achenes are small, 1.5–5 mm. long, narrow, terete or obtusely angled, and striate when dried. They are glabrous or provided with only a few short hairs, except in *P. gnaphalodes*, where they are long-villous. The hairs in this species project upward and usually exceed the achene in length. This feature is the only good single character separating *P. gnaphalodes* from *P. villosa* and *P. tagetina* in the areas where their distribution overlaps.

The pappus is made up of 6, occasionally 4 or 5, hyaline scales or squamellae. The squamellae may be entire or denticulate, obtuse or acute, unequal or equal in length, lanceolate to ovate in shape, and from less than one half to more than one half the length of the disk-flowers. In *P. tagetina* the pappus may range from one extreme to the other, and some of the scales may be obtuse while others in the same head may be acutish. In some of the species, such as *P. villosa*, *P. Bakeri*, and *P. gnaphalodes*, the pappus is fairly uniform. By itself it is a very unreliable taxonomic guide in this genus.

Other morphological features that should receive mention are the glands and the pubescence. All parts of the plant are frequently glandular-dotted. The stem of *P. sparsiflora*, which is much less villous than the stems of the other species, is quite often glandular. The tube of the disk-flowers may be dotted with these glands, and in some plants the glands extend onto the achene, and rarely they may be present on the pappus-scales. The ligules show the presence of these glands, particularly on the lower surface, and the leaves may show them in some number.

The pubescence, best described as woolly in most cases, is made up of long, multicellular hairs which frequently terminate in a small gland. The hairs of the achenes of *P. gnaphalodes* are very similar to those of other parts of the plant, but rarely terminate in a gland and are more frequently unicellular. The hairs on the squamellae of this species arise directly from the pappus-scales. The squamellae of other species are composed of elongated cells, the terminal ones ending more or less together, whereas in *P. gnaphalodes* some of the terminal cells give rise to hairs which extend beyond the scale. The pubescence of the stem and leaves tends to disappear with age.

DISCUSSION OF PROBLEMS AND RELATIONSHIPS OF SPECIES

In this study it was seen at once that *P. Cooperi* and *P. Bakeri* could be readily segregated from the other species. Even macroscopically they are seldom to be mistaken for any other species, many of which were labeled either *P. tagetina* or *P. gnaphalodes*. By separating the almost glabrous plants from these, with a

few exceptions, *P. sparsiflora* became evident. The distribution of this species in northern Arizona and southern Utah was of great help.

P. villosa is clear-cut in its northern range, but in Texas it is often difficult to distinguish from *P. tagetina* and *P. gnaphalodes*. However, on the basis of glabrous or villous achenes the plants which appeared alike to the naked eye could be placed in either *P. villosa* or *P. gnaphalodes*.

Those plants which did not fall into the above two species were placed in the "tagetina complex." The diversity of these plants in detailed character is not paralleled in other members of the genus. Nelson¹² noted this and commented, "the difference seems to be vegetative and not congenital." There seems to be no consistent basis for segregating this heterogeneous group except into the two varieties, *P. tagetina* var. *lanata* and *P. tagetina* var. *grandiflora*. Perhaps some future worker will see fit to split the "tagetina complex" into several species, but the writer believes that *P. tagetina* should be treated as a comprehensive specific unit.

The possibility of hybridization is strongly suggested, and on the basis of morphology and geography the following hybrids are conceivable:

P. tagetina x *gnaphalodes*

P. tagetina x *villosa*

P. villosa x *gnaphalodes*

P. tagetina x *sparsiflora*

Cytological studies might go a long way in throwing light on some of the problems of specific relationships. No chromosome counts for any species of this genus have been published, so far as the author is aware, and as he was unable to obtain living specimens he could not supply the information.

It is interesting but rather dangerous treading to try to draw conclusions regarding the phylogeny of *Psilostrophe* and its species. The most interesting speculation is in regard to the age of *P. gnaphalodes* as compared with the other species. If *P. gnaphalodes* is thought of as derived from one of the other species then we may claim to see the actual development of a hair-like pappus from a scale-like one. If, on the other hand, *P. gnaphalodes* is thought of as the archetype we might then use the evidence to show the development of a scale-like pappus from a hairy one. The writer is in sympathy with the former hypothesis, for it is his belief that the progenitor was a species that is now relatively constant in morphological features, a perennial rather than a biennial, and does not tend to hybridize.

The presence of close generic relatives helps very little in this problem, for the nearest genus is *Baileya*, in which a pappus is lacking.

Psilostrophe has been placed in the subtribe Riddellieae of the tribe Helenioideae by Gray¹³ and later botanists.¹⁴ The other two genera of the subtribe Riddellieae

¹² Nelson in Proc. Biol. Soc. Wash. 16:21. 1903.

¹³ Gray, Syn. Fl. N. Am. 12:71. 1884, and ed. 2, 1886.

¹⁴ Tribe Helenieae, subtribe Riddellinae. Engler & Prantl, Nat. Pflanzenfam. 4:253. 1890. Tribe Helenieae, subtribe Riddellianae. Rydberg in Britton, N. Am. Fl. 34:6. 1914.

are *Baileya* and *Whitneya*. The latter, a monotypic genus from California, is very distinct from the other two genera because of its opposite leaves, sterile disk-flowers, and absence of pappus. *Baileya*, on the other hand, is very closely allied to *Psilostrophe*; the principal taxonomic distinctions between the two are that *Baileya* lacks a pappus, usually has a greater number of ray and disk-flowers, and has bracts arranged in two more definite series.

GEOGRAPHICAL DISTRIBUTION

Psilostrophe is confined to southwestern North America, extending from southern Idaho in the north to San Luis Potosi in the south, from Texas in the east to San Bernardino County, California, in the west. The plants are found in ten of the United States and nine Mexican states. The greatest specific concentrations are in western Arizona and western Texas where three species each are found. *P. tagetina* and *P. gnaphalodes* have the widest known distribution of any of the species, while *P. sparsiflora* and *P. Bakeri* have the most restricted distribution. The plants are more or less xerophytic, preferring high, dry, sandy



Map 1. Showing distribution of *Psilostrophe Bakeri*, *P. sparsiflora*, *P. villosa* and *P. gnaphalodes*.

soil as a rule. Maps 1-2 show the distribution of the species and varieties of *Psilostrophe*.



Map 2. Showing distribution of *Psilostrophe Cooperi* and *P. tagetina* and its varieties.

ECONOMIC USES

The economic uses of *Psilostrophe*, as in the case of many *Compositae*, are very limited. Their chief value is probably as ornamentals. Parks¹⁵ says that *P. gnaphalodes* and *P. tagetina* make excellent border plants. However, *P. gnaphalodes* is poisonous to live stock. Further, he recommends that these two species be grown by nurserymen and made available to gardeners. Gray¹⁶, soon after the genus was described, pointed out that *P. tagetina* should "be very ornamental in cultivation."

P. gnaphalodes and *P. tagetina* are both very attractive plants, particularly var. *grandiflora* of *tagetina*, but both are excelled in beauty by *P. Cooperi*. This tall plant with its large papery rays makes a very striking appearance even on the herbarium sheet. In addition to this species, *P. sparsiflora* and *P. Bakeri* should make exceedingly fine perennials for cultivation.

¹⁵ Parks in Tex. Agr. Exp. Sta. Bull. No. 551, p. 160. 1937.

¹⁶ Gray in Mem. Am. Acad. II. 4:93. 1849.

COMMON NAMES

"Paperflower" is the most common name for this genus. Common names of the various species according to Kelsey and Dayton¹⁷ are as follows: "white-stem paperflower" for *Psilostrophe Cooperi*, "cudweed paperflower" for *P. gnaphadoles*, "greenstem paperflower" for *P. sparsiflora*, and "woolly paperflower" for *P. tagetina*. The last name, of course, could equally well apply to several of the species.

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ABBREVIATIONS

The herbaria cited in this paper are indicated by the following abbreviations:

FM—Chicago Museum of Natural History, formerly Field Museum of Natural History.

G—Gray Herbarium of Harvard University.

MBG—Missouri Botanical Garden.

PA—Philadelphia Academy of Natural Sciences.

T—University of Texas.

US—United States National Herbarium.

TAXONOMY

Psilostrophe DC. Prodr. 7:261. 1838; Greene, Pittonia 2:176. 1891; Britt. & Brown, Ill. Fl. 3:444. 1898, and ed. 2, 3:504. 1913; Britt. Man. 1005. 1901; Greene, Pl. Baker. 3:29. 1901; A. Nels. in Proc. Biol. Soc. Wash. 16:21. 1903; Small, Fl. Southeastern U. S., ed. 2, 1372. 1913; Rydb. in Britt. N. Am. Fl. 34:6. 1914; Jepson, Man. Fl. Pl. Calif. 1133. 1925; Rydb. Fl. Prair. and Plains, 852. 1932.

Riddellia Nutt. in Trans. Am. Phil. Soc. II. 7:371. 1841; Torr. & Gray, Fl. N. Am. 2:362. 1842; Gray in Mem. Am. Acad. II. 4:93. 1849; Gray in Proc. Am. Acad. 7:358. 1868; Benth. & Hook. Gen. Pl. 2:401. 1873; Gray, Syn. Fl. N. Am. 1²:71, 317. 1884, and ed. 2. 1886; Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. 4:253. 1890.

¹⁷ Kelsey & Dayton, Standardized Plant Names, p. 504. 1942.

DESCRIPTION OF THE GENUS

Perennial, rarely biennial, herbs or low shrubs, growing in clumps, from a tap root, 5 to 60 cm. in height; stem branching, pannose, densely villous, or glabrate. Lower leaves petioled, obovate to oblanceolate, entire or occasionally lobed, villous to glabrate, upper leaves alternate, smaller and sessile, spatulate to linear, rarely lobed. Involucre of 4–12 linear-oblong to lanceolate, villous, connivent bracts, and an inner series of 1–7 smaller scarious bracts, rarely an outer calyculate one. Receptacle naked. Inflorescence corymbose. Heads long-peduncled to subsessile. Ray-flowers pistillate, fertile, in a single series of 3–7. Ligules yellow, papery and persistent on the achenes, 3–16 mm. long, slightly 3–5-lobed. Disk-flowers hermaphrodite, fertile, regular. Corolla-tube with cylindric throat and 5 glandular lobes. Anthers obtuse at the base and acute at the apex. Style-branches of the ray-flowers capillary, of disk-flowers truncate at the tips. Achenes small, linear, more or less striate, obtusely angled or terete, glabrous or essentially so, or long-villous. Pappus of 4–6 nerveless hyaline squamellae, lanceolate to oval, acute to obtuse, equal or unequal in length. Leaves, stems, and parts of flower frequently glandular-granuliferous.

Type species: *Psilostrophe gnaphalodes* DC.

KEY TO THE SPECIES AND VARIETIES

- A. Stem white-pannose; shrubby plants; peduncles 3.0–8.0 cm. long..... 1. *P. COOPERI*
- AA. Stem villous to glabrate, gray to green; herbaceous plants; heads subsessile to long-peduncled.
 - B. Achenes and pappus long-villous; heads subsessile or with peduncles mostly less than 0.5 cm.; ligules about 6 mm. long..... 6. *P. GNAPHALODES*
 - BB. Achenes and pappus glabrous or essentially so; heads long-peduncled (subsessile only in *P. villosa*).
 - C. Involucre 7–10 mm. high, 4–6 mm. broad; ligules 4–6, 8–14 mm. long; pappus scales generally ovate, less than half the length of the disk-corolla..... 2. *P. BAKERI*
 - CC. Involucre 4–6 mm. high, 2–4 mm. broad; ligules 3–5, 3–11 mm. long; pappus scales rarely ovate, generally about half the length of the disk-corolla.
 - D. Heads densely clustered, on peduncles mostly less than 0.5 cm.; ligules 3–5 mm. long, deeply lobed..... 5. *P. VILLOSA*
 - DD. Heads loosely clustered, on peduncles mostly longer than 0.5 cm.; ligules 5 mm. or more long, shallowly lobed.
 - E. Plants glabrate to sparingly pilose; stem green, frequently slightly twisted..... 3. *P. SPARSIFLORA*
 - EE. Plants long-villous, rarely glabrate; stem gray to green, not twisted (except in *P. tagetina* var. *lanata*).
 - F. Ligules 5–9 mm. long; peduncles 0.5–2.0 cm. long; upper leaves about 1 cm. long or less..... 4. *P. TAGETINA*
 - FF. Ligules 6–12 mm. long; peduncles 1.0–4.0 cm. long; upper leaves frequently over 1 cm. long.
 - G. Plants densely villous, grayish, about 40 cm. high; basal leaves 5–15 cm. long, frequently lobed; pappus-scales generally acute..... 4a. *P. TAGETINA* var. *LANATA*
 - GG. Plants lightly villous, greenish, about 25 cm. high; basal leaves 3–6 cm. long, mostly entire; pappus-scales generally obtuse..... 4b. *P. TAGETINA* var. *GRANDIFLORA*

1. *Psilostrophe Cooperi* (Gray) Greene, *Pittonia* 2:176. 1891; Kuntze, *Rev. Gen. Pl.* 1:358. 1891; Rydb. in *Britt. N. Am. Fl.* 34:9. 1914; Rydb. *Fl. Rocky Mts.* 939. 1917; Jepson, *Man. Fl. Pl. Calif.* 1133. 1925; Munz, *Man. S. Calif. Bot.* 559. 1939; Blake in *Kearney & Peebles, U. S. Dept. Agr. Misc. Pub. No. 423, p. 969.* 1942 (as *cooperi*).

Riddellia Cooperi Gray in *Proc. Am. Acad.* 7:358. 1868; Gray, *Syn. Fl. N. Am.* 1²:318. 1884, and ed. 2, 1886.

A shrubby perennial with woody caudex; stems white-pannose, less densely so with age, 25 to 50 cm. high; lower leaves entire, linear, pannose to almost glabrate, 1–7 cm. long, seldom more than 2 cm. broad; upper leaves smaller and sessile; heads scattered; peduncles slender, 3.0–8.0 cm. long; involucre woolly, 6–8 mm. long, 4–5 mm. wide; ligules 4–8, 8–16 mm. long, nearly as broad, 3-lobed; disk-flowers 9–20; achenes glabrous; squamellae various, broadly oblong to lanceolate, erose to entire, obtuse to acute, generally from $\frac{1}{4}$ to less than $\frac{1}{2}$ the length of the disk-corollas.

Distribution: New Mexico to California into northwestern Mexico. Altitude: 2000–4000 ft.

ARIZONA.—COCHISE CO.: Benson, *Jones 25940* (MBG); Lowell, *Parish III* (G, MBG, NY, PA, US). GILA CO.: near Rock and Rye Creeks, *Collom 65* (MBG, NY), near Rye Creek, *479* (MBG); 17 mi. from Roosevelt on road to Payson, *Stone 60* (NY). GRAHAM CO.: Tanque, *Eggleston 19890* (US); Camp Grant, *Palmer 140* (G, MBG); Safford, 30 Sept. 1936, *Tharp* (T). GREENLEE CO.: near Clifton, 1 Nov. 1880, *Greene* (G, NY). MARICOPA CO.: New River Valley, 10 mi. s. of Canyon, *Gillespie 8690* (US). MOJAVE CO.: Kingman, 13 Aug. 1911, *Wooton* (US); southern tip of Cerbat Range, about 5 mi. s. w. of Kingman, *Barkley & Blondeau 4186* (MBG); 5 mi. s. w. of Kingman, *Rose 40083* (MBG); 10 mi. from Kingman on Peach Springs road, *Ferris & Duncan 2228* (NY); between Oatman and Kingman, *Degener 4907* (NY); plain near Oatman, April 1916, *Creighton* (PA); Fort Mojave, coll. of 1861, *Cooper* (G TYPE, US); Yucca, *Jones 3891* (FM, NY, PA, US); 30 mi. s. of Littlefield, *Maguire*, *Maguire & Maguire 5061* (G, MBG). NAVAJO CO.: Silver Lake, *Toumey 639a* (US). PIMA CO.: Tucson, *Demaree 8031* (MBG), *Fisher 155* (G), 11 Oct. 1894, *Hilzinger* (G, NY), *Lemmon Herbarium 46* (G), *Nelson & Nelson 1519* (G, MBG, NY, PA, US), 10 June 1908, *Sherff* (MBG), *Thornber 402* (MBG, NY, US), 16 April 1892, *Toumey s. n.*, *639b* (US), coll. of 1886, *Vasey* (US), and 1 May 1896, *Zuck* (US); near Tucson, *Peebles, Harrison & Kearney 1279* (US), *Pringle 9845* (NY), *Wiggins 6231* (US); west of Tucson, *Bartram 294* (PA); Picture Rocks, Tucson Mts., *Bartram 295* (US); w. of Tucson Mts., 19 Aug. 1927 and base of Tucson Mts. near Tucson, 24 July 1927, *Graham* (NY); low slopes Tucson Mts., *Bartram 296* (PA); few mi. w. of Carnegie Inst. Desert Lab., foothills of Tucson Mts., *Foster 509* (G); Saguaro Monument, 15 mi. e. of Tucson, *Brass 14330* (G, MBG); Martinez' Ranch, 16 mi. e. of Tucson, *Brass 14263* (G, MBG); between Sells and Tucson, *Gilman 215* (MBG, NY); Covered Wells, *Burnham 291* (FM, NY); Vail, 2 May 1937, *Darrow* (G); Rincon Pass, *Griffiths 2020* (NY); Baboquivari Mts., *Gilman 151* (NY), *Nelson & Nelson 1535* (MBG, NY, US); Tuviaucoc Hill, Tucson, *Harris C1476* (MBG, NY); roadside mine, *Harrison & Kearney 8667* (FM); San Salano, 10 Oct. 1925, *Peebles, Harrison & Kearney* (US); Camp Lowell, *Pringle 13755* (G, MBG, NY, PA). PINAL CO.: Ray, 1 May 1911, *Johnson* (NY). YAVAPAI CO.: Fort Whipple, *Coues & Palmer 254* (G, MBG); Castle Creek, *Toumey 639c* (US); Black Canyon Road near Agua Fria, *Wiegand & Upton 4474* (FM, MBG).

CALIFORNIA.—SAN BERNARDINO CO.: 1 mi. s. of Excelsior Talc Mine, Kingston Mts., Mojave Desert, *Abrams 14104* (G); Providence Mts., 24 May 1902, *Brandegee* (PA); e.

slope of Providence Mts., 29 May 1861, *Cooper* (US); Nipton, June 1915, *Brandegee* (G, FM, MBG, NY, US); Kelso, 2 May 1906, *Jones* (MBG, NY, US); Lanfair Valley, e. Mojave Desert, *Munz 13897* (FM); Seastalk, *Parish 10264* (G, MBG).

NEVADA.—CLARK CO.: Charleston Mts., Carpenter Canyon, *Anderson 7749* (NY, US); Valley of Fire, *Clokey 5952* (MBG, NY, T), *Maguire*, *Maguire & Maguire 5060* (G); Kyle Canyon, *Clokey 7367* (NY, US); Clark Creek, *Clokey 7369* (FM, NY, US); Kyle Canyon Fan, *Clokey 8177* (G, FM, MBG, NY, PA, T); Trout Creek Canyon Wash, *Clokey & Anderson 7368* (G, FM, NY); fan s. of Trout Creek, *Clokey & Anderson 8176* (G, FM, MBG, NY, PA); Virgin River, Bunkerville, *Goodding 752* (G, MBG); Moapi, *Kennedy 1127* (NY, US); 8 mi. w. of Goodsprings on road to Kingston, *La Rivers & Hancock 294* (MBG); 1 mi. w. of Riverside, *Maguire & Blood 4498* (FM, MBG); junction of Las Vegas and Head of Callville Wash, 2 mi. n. of airport, *Train 1804* (NY); junction of Kyle Canyon and Las Vegas Highway, *Train 1664* (PA). LINCOLN CO.: Searchlight, *Parish 10285* (NY). NYE CO.: Pahump Valley, *Coville & Funston 292* (US), *Purpus 6125* (PA, US).

NEW MEXICO.—MC KINLEY CO.: road near Zuni, *Schott III 91* (FM).

UTAH.—BEAVER CO.: Beaver, *Palmer 246* (G, MBG, NY, US).

MEXICO.—LOWER CALIFORNIA: San Luis, 22 April 1889, *Brandegee* (G, FM, US); Agua Dulce, *Brandegee* (FM); about 32 mi. from Rosario on road to San Augustine, *Ferris 8553* (US); San Augustine, *Gentry 4003* (MBG); El Marmol, *Harvey 518* (US); Los Angeles Bay, Gulf of California, *Palmer 538* (G, NY, US); coastal terrace along beach 24 mi. s. of Punto Prieta, *Wiggins 7737* (FM).

SONORA: District of Altar, 7 mi. s. of Sonoyta on road to Quitovac, *Keck 4147* (G, US).

2. *Psilostrophe Bakeri* Greene, Pl. Baker. 3:29. 1901; Rydb. Fl. Colo. 376. 1906; Coulter & Nels. New Man. Bot. Cent. Rocky Mts. 553. 1909; Rydb. in Britt. N. Am. Fl. 34:8. 1914; Fl. Rocky Mts. 939. 1917, and ed. 2. 1922.

Riddellia tagetina var. *pumila* M. E. Jones in Proc. Calif. Acad. II. 5:700. 1895.

P. pumila A. Nels. in Proc. Biol. Soc. Wash. 16:22. 1903.

A small perennial with woody caudex; stems long-villous, 5–30 cm. high; basal leaves spatulate to obovate, rarely lobed, long-villous, less than 10 cm. long; upper leaves smaller, spatulate to oblanceolate, entire; heads scattered; peduncles 2.0–5.0 cm. long; involucre generally lightly long-villous, 7–10 mm. long, 4–6 mm. wide, bracts apparent; ligules 4–6, 8–14 mm. long, 10 mm. wide, shallowly 3-cleft; disk-flowers 10–18; achenes glabrous; squamellae oval, obtuse, more or less erose, about $\frac{1}{3}$ the length of the disk-corolla.

Distribution: western Colorado to southern Idaho. Altitude: 4500–6500 ft.

COLORADO.—DELTA CO.: 30 June 1892, *Cowen* (NY); Hotchkiss, *Cowen 276* (US); Surface Creek, *Purpus 183* (FM); 8 mi. w. of Delta, *Rollins 1970* (G, NY); 2 mi. s. of Delta, *Rollins 2141* (G, MBG); 15 mi. w. of Delta, *Rollins 2155* (G). GARFIELD CO.: Rifle, *Osterhout 2127* (NY). MESA CO.: Grand Junction, *Baker 106* (G, MBG), *Jones 5474* (MBG, NY, US), and 22 May 1895 (US), *Saunders 405* (NY, US); Palisades, *Crandall 2995* (NY), May to August 1893, *Long* (G); Whitewater, *Rollins 1578* (G, MBG). MONTROSE CO.: Montrose, *Baker 14* (G, MBG, US), *Payson 658* (G); Uncompagre Mts. near Los Piños, coll. of 1878, *Flint* (NY).

IDAHO.—CASSIA CO.: near Strevell, *Warren 1416* (US).

UTAH.—KANE CO.: Paria (Pahria) Canyon, *Jones 5296* in part (MBG). GRAND CO.: near Grand Junction, 15 June 1900, *Stokes* (NY, US).

3. *Psilostrophe sparsiflora* (Gray) A. Nels. in Proc. Biol. Soc. Wash. 16:23. 1903; Rydb. in N. Am. Fl. 34:7. 1914; Rydb. Fl. Rocky Mts. 939. 1917; Blake in Kearney & Peebles, U. S. Dept. Agr. Misc. Pub. No. 423, p. 970. 1942.

Riddellia tagetina var. *sparsiflora* Gray, Syn. Fl. N. Am. 1²:318. 1884, and ed. 2. 1886.

P. tagetina var. *sparsiflora* Greene, Pittonia 2:176. 1891.

P. divaricata Rydb. in Britt. N. Am. Fl. 34:8. 1914, in part.

P. grandiflora Rydb. loc. cit. 8. 1914, in part.

A perennial; stems pilose to glabrate above, often glandular-dotted, frequently twisted, 15–45 cm. high; basal leaves spatulate to linear, seldom lobed, very loosely villous, 5–10 cm. long, rarely wider than 1.5 cm.; upper leaves smaller, linear or linear-oblongate, and sessile; heads generally few in loose corymbs; peduncles slender, 0.5 cm. or longer; involucre lightly woolly, about 5 mm. long, 3 mm. wide; ligules usually 3, 6–8 mm. long and noticeably wider, shallowly 3-lobed; disk-flowers 10 or less; achenes essentially glabrous to glabrous; squamellae unequal, linear-lanceolate, mostly acute, $\frac{1}{2}$ – $\frac{2}{3}$ the length of the disk-corolla.

Distribution: eastern New Mexico and southern Utah to northern Arizona. Altitude: 3000–6000 ft.

ARIZONA.—APACHE CO.: Navajo Reservation, *Vorbies* 56 (G, MBG, NY). COCONINO CO.: Grand Canyon, Aug. 1897, *Allen* (NY), *Eastwood* 3692, 5816 (G), Feb.-May 1885, *Gray* (G), 1 July 1915, *Hitchcock* (US), 51, 77 (US), *Knowlton* 272 (US), *Toumey* 638 (US); Boucher Creek, *Wiegand & Upton* 4475 (FM); Le Conte Plateau, 16–19 Oct. 1906, *Pilsbry* (PA); 2 mi. s. of Grand Canyon, *Degener & Park* 4411 (NY); $\frac{1}{2}$ mi. e. of Grand Canyon National Park, *Ferris* 10213 (G); s. rim of Grand Canyon, 25 mi. n. w. of Cameron, *Carter* 1429 (MBG, NY); near Cameron, *Hanson* A55 (FM, MBG, PA, T); 42 mi. e. of El Tovar on road to Cameron, *Peebles* 13332 (US); Lee's Ferry, Paria [Pahria] Canyon, *Cutler* 3135 (NY, MBG); Coconino Forest at Deadman Ranger Station, *Eggleston* 17187 (MBG); Falls of the Little Colorado River, *Fulton* 7359 (US); 3 mi. n. of the Navajo Bridge, *Rollins & Chambers* 2440 (G); 12 mi. s. w. of Tanner's Crossing, 1 June 1901, *Ward* (NY); O'Leary Peak, *Goldman* 2893 (US); Flagstaff, 5 Aug. 1922, *Hanson* (US), 7–11 Aug. 1915, *Hitchcock* (US), *MacDougal* 229 (G, NY, PA, US), May-Oct. 1901, *Purpus* (MBG, US); near Flagstaff, *Leiberg* 5624 (US); 20 mi. n. of Flagstaff, 16 July 1943, *Huffman* (NY); 10 mi. e. of Jacob Lake, 16 July 1943, *Huffman* (NY); along U. S. Highway #66 between Peach Springs and Hyde Park, *Heller* 15777 (MBG, NY); Cosnino, *Jones* 4038 (NY); below Nagle's Ranch, *Jones* 6050a (US); San Francisco Mts., *Knowlton* 182 (US); w. of Echo Cliffs, *McKelvey* 4454 (G); Wupatki National Monument, *Whiting* 756/892 (US). MOHAVE CO.: n. end of Toroweap Valley, *Cottam* 6589 (MBG); Peach Springs, *Degener* 4900 (NY); 6 mi. w. of Peach Springs, *Kearney & Peebles* 12741 (US); Trumbull, *Palmer* 246 $\frac{1}{2}$ (G, MBG, NY, US); Johnson's Canyon, *Rusby* 657 (FM, MBG, NY, US) and 4734 (MBG, US). NAVAJO CO.: Laguna Canyon, Keet Leil Ruin, *Clute* 24 (G, MBG, NY, US), and 24a (NY); Betatakin, *Eastwood & Howell* 6604 (US); s. of Winslow, *Peebles* 9539 (US).

NEW MEXICO.—COUNTY NOT DETERMINED: Mesa la Vecas, 18 Sept. 1883, *Marsh* (US); no locality given, coll. of 1867, *Parry* (US).

UTAH.—GARFIELD CO.: *Siler* (PA). KANE CO.: Pahria Canyon, *Jones* 5296 in part (MBG, NY, US); 10 mi. s. of Pahria, *Jones* 5291i (US); 2 mi. n. e. of Kanab to Red Canyon, *Stone* 276 (NY); Kanab, coll. of 1872, *Thompson* (G, MBG). COUNTY NOT DETERMINED: *Bishop* (G TYPE, FM); *Vasey* (FM); Cainville, *Jones* 5696 (US).

4. *Psilostrophe tagetina*¹⁸ (Nutt.) Greene, *Pittonia* 2:176. 1891; Britt. & Brown, Ill. Fl. 3:444. 1898 (as "*Tagetinae*"); A. Nels. in Proc. Biol. Soc. Wash. 16:22. 1903; Rydb. Fl. Colo. 376. 1906; Coult. & Nels. New Man. Bot. Cent. Rocky Mts. 553. 1909; Rydb. in Britt. N. Am. Fl. 34:8. 1914 (as "*Tagetinae*"); Rydb. Fl. Rocky Mts. 939. 1917 (as "*Tagetinae*"); Blake in Kearney & Peebles, U. S. Dept. Agr. Misc. Pub. No. 423, p. 969. 1942 (as "*tagetinae*").

Riddellia tagetina Nutt. in Trans. Am. Phil. Soc. II. 7:371. 1841 (as "*Tagetinae*," sphalm.); Torr. & Gray, Fl. N. Am. 2:362. 1842; Torr. in Emory, Notes Mil. Reconnois. p. 143, *pl.* 5. 1848; Gray in Mem. Am. Acad. II. 4:94. 1849; Gray, Syn. Fl. N. Am. 1²:317. 1884, and ed. 2. 1886.

P. Hartmanii Rydb. in Britt. N. Am. Fl. 34:8. 1914.

P. divaricata Rydb. *loc. cit.*, in part.

A perennial, generally woody at the base; stems densely to lightly villous, occasionally glabrate, 10–50 cm. high; basal leaves ovate to oblanceolate, usually spatulate, entire or pinnately lobed, densely to lightly villous, 2–10 cm. long, less than half as wide; upper leaves linear to oblanceolate, smaller and greener than the basal leaves; heads generally numerous in dense to loose corymbs; peduncles usually 0.5–2.0 cm. long; involucre usually densely woolly, 5–6 mm. long, 3–4 mm. wide; ligules 3–5, 5–9 mm. long, 3 (rarely 4 or 5) shallowly lobed; disk-flowers 6–12; achenes glabrous or with a few short and scattered hairs; squamellae various, lanceolate to lance-elliptic, obtuse to acute, entire to erose, and from $\frac{1}{3}$ to $\frac{2}{3}$ the length of the disk-corolla.

Distribution: western Texas to eastern Arizona into northern Mexico. Altitude: 3000–8000 ft.

ARIZONA.—APACHE CO.: White Mts., Hondo Hill, 28 July 1905, *Wootton* (US); Adamana to "Long H" Ranch, *Griffiths* 5173 (US). COHISE CO.: Chiricahua Mts., Paradise, 4 July 1937, *Darrow* (G); Portal to Paradise, *Eggleston* 10650 (US); desert between the Chiricahuas and the Southern Pacific Railroad, 6 mi. s. of Dos Cabezas, *Stone* 184 (PA); Camp Bowie, *Rothrock* 463 (FM, G, PA, US). GREENLEE CO.: San Francisco Mts. (?), 21 July 1864, *Anderson* (MBG). COUNTY NOT DETERMINED: Moki Reservation and Little Colorado River, *Hough* 115 (US).

NEW MEXICO.—BERNALILLO CO.: 10 mi. w. of Albuquerque, *Rollins & Chambers* 2418 (G). CATRON CO.: Beaverhead, *Eggleston* 20399 (G); Mangas, *Smith* 25 (US), 19 Oct. 1897, *Metcalf* (US); Reserve, 9 July 1906, *Wootton* (G); Mogollon Mts., Gila Hot Springs, 20 Aug. 1900, *Wootton* (US); Tularosa Creek, 8.4 mi. w. of the Continental Divide on the road from Magdalena to Reserve, *Goddard* 810 (MBG). CHAVES CO.: Roswell, *Earle & Earle* 374 (MBG, NY, US); 20 mi. s. of Roswell, 20 Aug. 1900, *Earle & Earle* (NY); Arroyo Ranch near Roswell, *Griffiths* 5741 (MBG). COLFAX CO.: Raton Mts., Aug. 1867, *Bell* (MBG, PA). DONA ANA CO.: s. w. Pyramid Peak, *Fosberg* S3318 (G, MBG, US); w. of Organ Mts., 1 May 1906, *Standley* (MBG); Organ Mts., Van Patten's, 11 June 1906, *Standley* (US); Tortugas Mt., *Standley* 6445 (US); Los Cruces, *Wootton* 6 (G, MBG, NY, US); Mesilla Valley, *Wootton & Standley* 3320 (FM, MBG, NY), 1 June 1906, *Standley* (MBG), May 1906, *Wootton* (T); Mesilla Park, 23 May 1900, *Cockerell* (NY); Doñana, *Wislizenus* 82 (G, MBG); Strauss' Station, *Mearns*

¹⁸ Nuttall's spelling in the original work, "*Tagetinae*," which is gramatically incorrect, is probably a misprint. In letters to the author, Mr. C. A. Weatherby and Dr. S. F. Blake are of the opinion that the spelling "*tagetina*" should be used as was done by Torrey and Gray, *loc. cit.*

1525 (US); between Strauss and Anapra, *Stearns* 384 (US); Monument #40, Mexican Boundary Line, *Mearns* 253 (US). EDDY CO.: Pecos Valley near Texas line, *Bailey* 746 (US); Dark Canyon, Rocky Arroyo Road, 45 mi. n. w. of Carlsbad, *Grassel* 26 (FM); near Loving, *Standley* 40359 (US); near mouth of South Fork, Guadalupe Mts., *Wilkins* 1790 (PA). GRANT CO.: Wind Canyon, 7-8 mi. n. of Cliff, *Eggleston* 16538 (FM, MBG); near Santa Rita del Cobre, coll. of 1877, *Greene* (FM); plains of the Gila, 2 July 1880, *Greene* (PA); Fierro to Santa Rita, 27 Aug.-12 Sept. 1911, *Holzinger* (MBG, US); Mangas Springs, 18 mi. n. w. of Silver City, *Metcalfe* 124 (G, MBG, NY), and 648 (MBG, NY, US); near Pinos Altos, 26 June 1936, *Stewart* (MBG); Bear Mt., 5 mi. from Silver City, *Wolf* 2623 (G). GUADALUPE CO.: Santa Rosa, *Whitehouse* 7314 (T); 8 mi. s. of Santa Rosa, *Hubricht*, *Shoop* & *Heinze* (MBG). LINCOLN CO.: Lincoln, 31 July 1900, *Earle* & *Earle* (NY); 5 mi. w. of Lincoln, *Hitchcock*, *Rethke* & *van Raads-booven* 4276 (G). MCKINLEY CO.: Fort Defiance, *Friese* (PA); Camp #1, Rio Zuni, 24 Sept. 1851, *Woodhouse* (PA). OTERO CO.: *Archer* 7303 (NY), 7304 (NY, PA); Mesalero, 3 Aug. 1931, *Huber* (PA); Sacramento Mts., Alamo Canyon, 8-10 Oct. 1932, *Pilsbry* (PA); 4 mi. above Tularosa, *Wootton* & *Standley* 3615 (US). QUAY CO.: Nara Vista, *Fisher* 3 (US); Tucumcari, *Fisher* 30 (US). RIO ARriba CO.: near El Rito, *Rusby* 175½ (PA). SANTA FE CO.: Galisteo, vicinity of Santa Fe, *Arsène* & *Benedict* 15817 (PA); 10 mi. w. of Santa Fe, *Heller* & *Heller* 3739 (G, MBG, NY, US). SANDOVAL CO.: Jemez Springs, *Nelson* 11671 (G, MBG); Algodones, *Rothbrock* 82 (FM). SAN MIGUEL CO.: Las Lagunitas, 14 mi. s. of Las Vegas, *Brandee* 11794 (MBG). SIERRA CO.: Lake Valley, coll. of 1914, *Beals* (US); road from Kingston to Tierra Blanca, *Eggleston* 16323 (FM, G, NY). SOCORRO CO.: between Nogal Canyon and San Marcial, *Ferris* & *Duncan* 2348 (MBG); Magdalena, *Herrick* 651 (FM); Water Canyon, Magdalena Mts., *Herrick* & *Herrick* 108, 137 (FM). TAOS CO.: Barranca Station, 28 Aug. 1894, *Smith* (PA); near Barranca, 28 Aug. 1894, *Smith* (PA). VALENCIA CO.: Cebolla Springs, *Bailey* 1072 (US); Laguna, *Collins* 11 (PA); e. of Laguna Pueblo on Highway #66, *Nelson* & *Nelson* 2179 (MBG). COUNTY NOT DETERMINED: 66 mi. e. of Albuquerque, 14 July 1943, *Huffman* (NY). NO LOCALITY GIVEN: *Fendler* 461 (FM, G, MBG, NY, PA, US).

TEXAS.—BREWSTER CO.: Panther Springs, *Marsh* 79 (FM); Chisos Mts., *Mueller* 8231 (G, MBG, NY, T), 22-24 Nov. 1922, *Pilsbry* (PA); Willow Creek and Green Gulch Canyons, *Sperry* 250 (US); Lower Green Gulch, *Warnock* 1232 (G); Mesa de Anguila, *Warnock* 726 (US), 13 Aug. 1915, *Young* (MBG, T); Rock Spring Canyon, 24 Aug. 1915, *Young* (T); banks of Rio Grande in Grand Canyon near Castellan, *Palmer* 34216 (NY). CONCHO CO.: Rio Concho, *Thurber* 76 (G, NY). CULBERSON CO.: 9 mi. e. of Van Horn, *Waterfall* 4149 (G); 40 mi. n. e. of Van Horn, *Waterfall* 5008 (G); 1.5 mi. e. of Daughtery, *Waterfall* 5181 (G); Guadalupe Mts., *Bailey* 701 (US), 15 Aug. 1916, *Young* (T), 28 Aug. 1916 (MBG); Pine Springs, *Cory* 17611 (G); Miller Brothers Ranch, *Cory* 2695 (G). EL PASO CO.: coll. of 1858, El Paso, *Dieffen-derfer* (PA), *Fisher* 173 (MBG), *Rose* 1193 (G, US); w. of El Paso, 15 June 1891, *Dewey* (US); n. of El Paso, *Ferris* & *Duncan* 2380 (MBG); 1.5 mi. s. of Newman, *Waterfall* 3940 (G); along Highway #62, between El Paso and Hueco, 6-16 mi. e. of El Paso, *Waterfall* 3888 (G); in Hueco Mts., near Highway #62, *Waterfall* 3928 (G). HUDSPETH CO.: 2 mi. w. of Salt Flats, *Waterfall* 3846 (G); vicinity of Ft. Quitman, *Waterfall* 3994 (G); 3 mi. e. of Sierra Blanca, *Waterfall* 4017 (G); 4 mi. w. of Sierra Blanca, *Ferris* & *Duncan* 2488 (MBG, NY); Ft. Hancock, 23 June 1891, *Evans* (MBG). JEFF DAVIS CO.: near Ft. Davis, *Palmer* 32083 (MBG, PA, T); Ft. Davis, *Blake* (NY); Davis Mts., near Rockpile Ranch, 21 Aug. 1940, *Hinckley* (G). MAVERICK CO.: Eagle Pass, 10 Nov. 1893, *Plank* (NY). MITCHELL CO.: *Goldstein* (PA). PRESIDIO CO.: Marfa, *Eggleston* 17285 (G, NY), *Hinckley* 652 (FM, T); near Marfa, *Drusbel* 10499 (PA). REEVES CO.: vicinity of Pecos, *Gillespie* 5263 (G, US). WARD CO.: Barstow, *Earle* & *Tracy* 42 (NY), *Tracy* 8164 (NY, T, US), *Earle* 643 (NY); Pyote, 19 May 1900, *Williams* (US). COUNTY NOT DETERMINED: road between El Paso and Hueco, N. Mex., *Mulford* 111 (MBG, NY); Comanche Plains, 2 Sept. 1853, *Bigelow* (US); along Rio Grande, *Hayes* 469 (FM, NY).

MEXICO.—CHIHUAHUA: Ciudad Juarez, *Pringle* 9954 (G, MBG, NY, US); valley around Juarez, 1912, *Stearns* (MBG); foothills of the Sierra Madre, near Colonia Juarez, *Nelson* 6319 (G, US); Colonia Diaz, *Nelson* 6441 (G, US); Chihuahua, *Le Sueur* 54 (FM, G, T); near Laguna de Guzman, *Hartman* 726 (G); Casas Grandes, *Hartman* 807 (FM, G, NY, PA, US); near Casas Grandes, *Townsend & Barber* 364 (MBG, NY, US); 1 mi. e. of Pozo de Villa on Coahuila boundary, *Johnston* 8183 (G); Sierra San Carlos, *Johnston & Muller* 67 (G); Cañon del Rayo, Sierra del Diablo, *Stewart* 884 (G); 4 km. n. of Fierro, Sierra de Encinillas, *Stewart* 801 (G).

COAHUILA: Muzquiz, 20 mi. n. w. of Hacienda La Babia, *Wynd & Mueller* 432 (G, MBG, NY, US); Municipio de Cuatro Cinegas, Rancho Falcon, Cuesta del Dulce, about 12 mi. w. of Hacienda Berrendo, *Wynd* 723 (G); near Otto, 6 Sept. 1906, *Johnson* (US); base of Picacho del Fuste, *Johnston* 8437 (G); Sierra de las Cruces, Santa Elena Mines, *Johnston & Muller* 1382 (G); n. e. from Tanque Armendais, *Johnston & Muller* 760 (G); Del Carmen Mts., *Marsh* 901 (FM, G); Sierra de Santa Rosa, *Marsh* 1233, 1340, 1522 (G); Sierra del Carmen, *Stewart* 1572 (G); 3 km. s. of El Tule, *Stewart* 544 (G); 2 km. n. of Agritos, *Stewart* 1273 (G); western base of Sierra de los Guajes, 4 km. e. of Rancho Buena Vista, *Stewart* 1485 (G); 8 km. n. w. of Santa Elena, *Stewart* 2161 (G).

STATE NOT DETERMINED: chiefly in the Valley of the Rio Grande below Doñana, *Mexican Boundary Survey* 628 in part (NY, US); near Olla, near the banks of the Rio Grande, *Wislizenus* 36 (MBG); Long's Expedition, *James* (G).

4a. *Psilostrophe tagetina* var. *lanata* A. Nels. in Proc. Biol. Soc. Wash. 16:22. 1903.

P. lanata Anon. in Proc. Biol. Soc. Wash. 16:186 (Index). 1903; Rydb. in Britt. N. Am. Fl. 34:8. 1914.

Densely villous on the caudex, stems generally long-villous, gray, thick, occasionally twisted, mostly 40 cm. high; basal leaves spatulate, frequently lobed, long-villous, 5–15 cm. long; upper leaves linear-oblong to spatulate, occasionally lobed, 1–7 cm. long; peduncles mostly 1.0–3.0 cm. long; involucre 6–7 mm. long, 3–4 mm. wide; ligules 3–5, 6–12 mm. long; squamellae lance-elliptic to oblong, rarely lanceolate, acute to obtuse; otherwise as in the species.

Distribution: western Texas to southern Utah into northern Mexico.

NEW MEXICO.—EDDY CO.: Guadalupe Mts., South Fork, *Wilkens* 1738 (PA). OTERO CO.: Hueco, 23 Aug. 1911, *Barlow* (FM); no locality given, 7 April–24 May 1902, *Rebn & Viereck* (PA), 21–28 May, *Viereck* (PA). SOCORRO CO.: Magdalena, *Herrick* 643 (US).

TEXAS.—BREWSTER CO.: Boquillas, *Hanson* 608 (MBG, US), and 650 (US); Santa Helena Canyon, Rio Grande, *Innes & Warnock* 501 (G); between Marathon and Persimmon Gap, *McKelvey* 1974 (G), and 1980 (G, US); e. of Chisos Mts., *Sperry* 1709 (G). CULBERSON CO.: Kent, *Tracy & Earle* 42 (G, NY, T, US). EL PASO CO.: *Jones* 3718 (NY, PA, US), *Meebold* 22544 (NY), and coll. of 1881, *Vasey* (G); Fort Bliss, 30 April 1915, *Carlson* (G, NY). HUDSPETH CO.: Sierra Blanca, *Jones* 25943 (MBG).

UTAH.—SAN JUAN CO.: 10 mi. s. of Moab, 4 July 1942, *Huffman* (NY).

MEXICO.—CHIHUAHUA: Valley of the Rio Grande, Paso del Norte, *Pringle* 71 (G, NY, PA, US); hills near Chihuahua, *Pringle* 71½ (MBG, NY); vicinity of Chihuahua, *Palmer* 164 (FM, G, MBG, NY, US); Santa Eulalia, 18 Aug. 1885, *Wilkinson* (US).

COAHUILA: Sierra Mojada Mts., *Jones* 285 (US).

STATE NOT DETERMINED: Valley of the Rio Grande below Doñana, *Mexican Boundary Survey* 629 (US CO-TYPE).

4b. *Psilostrophe tagetina* var. *grandiflora* (Rydb.) Heiser, n. comb.

P. grandiflora Rydb. in Britt. N. Am. Fl. 34:8. 1914, in part.

P. sparsiflora Blake in Kearney & Peebles, U. S. Dept. Agr. Misc. Pub. No. 423, p. 970. 1942, in part.

Stems green, lightly villous, 25 cm. or taller; lower leaves spatulate, generally entire, lightly villous, 3–6 cm. long; upper leaves linear to spatulate, 1–5 cm. long, entire, green; peduncles slender, 1–4 cm. long; involucre 6 mm. long, 3–4 mm. wide; ligules broad, 7–12 mm. long; squamellae lance-elliptic to lance-oblong, obtuse, rarely acutish, $\frac{1}{2}$ or less the length of the disk-corolla; otherwise as in the species.

Distribution: with the species in southeastern Arizona and southwestern New Mexico.

ARIZONA.—COCHISE CO.: Chiricahua Mts., near Cedar Gulch, Paradise, *Blumer 1709* (G, MBG TYPE COLLECTION), and 88 (US); Silver Creek, about Portal, *Eggleston 10945* (G, US); Apache Pass, Sept. 1881, *Lemmon Herbarium* (FM); Fort Bowie, 3–30 Nov. 1906, *Pilsbry* (PA).

NEW MEXICO.—GRANT CO.: Apache Tejo, *Mulford 941* (MBG, NY). HIDALGO CO.: e. side of San Luis Mts., *Mearns 2186* (NY); Animas Creek, *Metcalf 1144* (G, NY, US). SOCORRO CO.: Socorro, May 1881, *Vasey* (US).

5. *Psilostrophe villosa* Rydb. in Britton, Man. 1006. 1901; Britt. & Brown, Ill. Fl. ed. 2, 3:504. 1913; Small, Fl. Southeastern U. S. ed. 2, 1372. 1913; Rydb. in Britt. N. Am. Fl. 34:7. 1914; Rydb. Fl. Prair. & Plains, 852. 1932; Stemen & Meyers, Okla. Fl. 594. 1937.

P. cerifera A. Nels. in Proc. Biol. Soc. Wash. 16:21. 1903.

P. cerifera var. *biennis* A. Nels. loc. cit.

P. biennis Anon. in Proc. Biol. Soc. Wash. 16:186 (Index). 1903.

A biennial or perennial; stems loosely to densely long-villous, 10–60 cm. high; basal leaves spatulate to oblanceolate, entire, or some 3–5-lobed, short-petioled, 5–10 cm. long; upper leaves smaller and sessile, rarely lobed; heads several in a small congested corymb, on peduncles less than 0.5 cm. long, or subsessile; involucre densely woolly, 5 mm. long, 3 mm. wide; ligules 3–4, 3–5 mm. long, 3-lobed about half of their length or sometimes 4-lobed; disk-flowers 5–12, usually 6–8; achenes glabrous or essentially so; squamellae linear-lanceolate, acute, $\frac{1}{2}$ or over the length of the disk-corolla.

Distribution: southern Kansas to Texas and eastern New Mexico. Altitude: 500–5000 ft.

KANSAS.—BARBER CO.: *Hitchcock 741* (G, MBG, NY, US). CLARK CO.: near Sitka, *Palmer 41863* (MBG); on Cimarron, 8 mi. s. of Sitka, *Rydberg & Imler 1120* (NY). COMANCHE CO.: 8 mi. w. of Coldwater, *Rydberg & Imler 716* (MBG, NY). MEADE CO.: Meade, July 1892, *Hitchcock* (MBG), 26 June 1888, *Kellerman* (MBG, NY, PA, US); 7 mi. w. of Meade, *Rydberg & Imler 796a* (NY); near Crooked Creek, *Smyth 140* (NY).

NEW MEXICO.—COUNTY NOT DETERMINED: Upper Canadian, April 1848, *Gordon* (MBG); no locality given, *Heary* (PA), *Wright 1259* (G, NY, PA).

OKLAHOMA.—CUSTER CO.: 2 mi. w. of Weatherford, *Hubricht, Shoop & Heinze B1389* (MBG); 1 mi. w. and 1 mi. s. of Weatherford, *Waterfall 5511* (G); Weatherford, 18 May 1937, *Waterfall* (NY). ELLIS CO.: near Shattuck, *Clifton 3200* (G). HARMON CO.: near Hollis, *Stevens 1052* (G). HARPER CO.: near Horbick's, *Stevens 258½* (G). MAJOR CO.: near Waynoka, *Stevens 593* (G); Glass Mts., *White 141* (MBG, NY), and

164 (MBG). WASHITA CO.: near Rocky, *Stevens* 973 (G). WOODS CO.: near Fairvalley, *Stevens* 715 (G, MBG, NY, US), and 1637 (G).

TEXAS.—BAILEY CO.: Coyote Lake, *Ferris & Duncan* 3459 (MBG); 1 mi. n. w. of Muleshoe, *Cory* 37520 (G). BAYLOR CO.: Seymour, *Reverchon* 505 in part (MBG, US). BREWSTER CO.: Marathon, 14 June 1931, *Tharp* 286 (MBG, NY, T). BRISCOE CO.: Quitaque, 29 April 1934, *Tharp* (NY, T); Floyds Crossing, Tule Creek, *Reed & Demaree* 7636 (US). CALDWELL CO.: Clear Fork, 10 May 1858, *Hayes* (NY). CHILDRESS CO.: 11 mi. n. of Childress, *Innes & Moon* 1004 (G). COKE CO.: 1.5 mi. s. w. of Silver, *Cory* 5322 (G); Fort Chadbourne, 1856, *Swift* (PA). DALLAM CO.: 6 mi. w. of Dallam, *van Gorder* 49 (T). DAWSON CO.: 8 mi. n. of Lamesa, *Innes & Moon* 1061 (G). DONLEY CO.: 5¾ mi. n. w. of Memphis, *Cory* 13478 (G). FISHER CO.: Rotan, April and May 1933, *Brookes* (T). FLOYD CO.: Quitaque-Plainview Road, *Ferris & Duncan* 3371 (MBG). GARZA CO.: near the "Cap Rock", *Ruth* 1283 (US). HALL CO.: Estelline, 8 and 9 July 1903, and 23 May 1904, *Reverchon* (MBG). HEMPHILL CO.: on Canadian, 10 Aug. 1900, *Eggert* (MBG). HOWARD CO.: Big Spring[s], *Bray* 416 (T, US), *Letterman* 25 (MBG, US). HUDSPETH CO.: Salt Basin, 6 Aug. 1916, *Young* (T). HUTCHINSON CO.: July 1934, *Shepard* (T). JEFF DAVIS CO.: Davis Mts., 13 Aug. 1914, *Young* (T). LISCOMB CO.: Liscomb, *Howell* 51, 52 (US). LIVE OAK CO.: *Schulz* 38-39 (FM), 27 June 1941, *Tharp* (T). LUBBOCK CO.: Boll's Ranch, 10 mi. s. e. of Lubbock, *Demaree* 7668 (G, MBG, US); Johnson's Ranch, Lubbock, *Reed* 3408 (US); vicinity of Lubbock, *Reed* 3094 (US); Posey, *Demaree* 7572, 7773 (US). MITCHELL CO.: on Colorado, 8, 9, and 10 June 1900, *Eggert* (MBG); Colorado, *Tracy* 7875 (G, NY, T, US); Loraine, *Finley* 3 (T). NOLAN CO.: Sweetwater, 22 June 1891, *Evans* (MBG), *Palmer* 12472, 13050 (MBG); near Blackwell, *Palmer* 34573 (MBG, PA, US). POTTER CO.: Amarillo Creek, *Reverchon* 3328 (MBG). RANDALL CO.: Palo Duro Canyon, *Ball* 1222, *Cory & Ball* 1709 (US), *Reverchon* 3328A (M); Canyon [City], *Palmer* 12520 (MBG, US), 14049 (MBG), 13 Aug. 1900, *Eggert* (MBG), 5 Aug. 1903, *Reverchon* (MBG). REAGAN CO.: *Cory* 4666 (G); 15 mi. n. w. of Stiles, *Cory* 15195 (G); Best, May 1931, *Graves* (T). REEVES CO.: 3 mi. w. of Pecos, *Waterfall* 4383 (G). SAN PATRICIO CO.: 5 April 1932, *Tharp* (T). TAYLOR CO.: April 1882, *Reverchon* 505 in part (FM, US). TERRELL CO.: near Feodora, *Palmer* 33542 (NY). TERRY CO.: Brownfield, *Reed* 3799 (T). VALVERDE CO.: high bridge of the Pecos, 27-28 April 1903, *Pilsbry* (PA); Del Rio, 22-23 April 1903, *Pilsbry* (PA); near Del Rio, *Palmer* 11088 (MBG, PA, US); Devils River, *Orcutt* 6028 (MBG). WEBB CO.: Toga, 1883, *Holstein* (PA). WICHITA CO.: *Boll* 505 (FM). COUNTY NOT DETERMINED: Fort Smith to Rio Grande, Comanche Plains, *Bigelow* 2 (NY).

6. *Psilostrophe gnaphalodes* DC. Prodr. 7:261. 1838; A. Nels. in Proc. Biol. Soc. Wash. 16:20. 1903; Rydb. in Britt. N. Am. Fl. 34:7. 1914.

Riddellia arachnoidea Gray in Mem. Am. Acad. II. 4:94. 1849; Gray, Syn. Fl. N. Am. 1²:318. 1884, and ed. 2, 1886; Coulter in Contr. U. S. Nat. Herb. 2:226. 1892.

R. gnaphalioides O. Hoffm. in Bull. Herb. Boiss. 3:628. 1895.

A biennial; stems rather densely villous, 10-50 cm. high; basal leaves spatulate to oblanceolate, occasionally lobed, loosely long-villous to pannose, up to 8 cm. long and 2 cm. wide; upper leaves smaller, oblanceolate to linear; heads several in a congested corymb, on peduncles less than 0.5 cm. long to sessile; involucre densely woolly, 5-6 mm. long, 3 mm. wide; ligules 3-4, 5-7 mm. long, slightly 3-lobed; disk-flowers 8-12; achenes and squamellae of the pappus densely long-villous; squamellae subulate to lanceolate, acute, about ½ the length of the disk-corolla.

Distribution: southern Texas to central Mexico. Altitude: 1000-7000 ft.

TEXAS.—BRAZOS CO.: College Station, 10 June 1891, Dewey (US). BREWSTER CO.: Stewart's, *Cory* 2688 (G); 60 mi. s. of Alpine, Innes & Moon 1168 (G); near Alpine, Palmer 30590a (MBG); Alpine, Sperry T340 (US), Wiegand & Wiegand 2597 (G); Terlingua, Reed 1811 (US); between Terlingua and Marathon, Schulz 3001 (FM); Marathon, von Schrenk 37, 42 (MBG); s. of Santiago Peak, Ferris & Duncan 2757 (MBG); Chisos Mts., Sperry 743 (US), 24 Aug. 1915, Young (T). CULBERSON CO.: Van Horn Flats, 7 and 10 July 1900, Eggert (MBG); 7 mi. n. of Van Horn, Waterfall 5125 (G); 9 mi. s. w. of Van Horn, Waterfall 4681 (G); s. of Eagle Mt., Waterfall 4437 (G). DIMMIT CO.: Carrizo Springs, Hoaglund 7303, 7313 (T). EL PASO CO.: e. of El Paso, 21 May 1898, Bray (T). HUDSPETH CO.: Indian Hot Springs, Jones 36415 (MBG); 6 mi. n. e. of Indian Hot Springs, Waterfall 4837 (G). JEFF DAVIS CO.: Limpia, 16 May 1915, Allen (T); 2.8 mi. n. of Fort Davis, *Cory* 17685 (G); Davis Mts., between Little and Big Aguja Canyons, Moore & Steyermark 3114 (G, MBG, PA, US); n. edge of Davis Mts., 5 mi. e. of Kent, Rollins & Chambers 2757 (G); Davis Mts., Tracy & Earle 208 (T, US). KENNEDY CO.: 6 Aug. 1925, Tharp (T). MAVERICK CO.: Eagle Pass, 25 May 1898, Bray (T); 10 mi. e. of Eagle Pass, 9 May 1898, Bray (T). MONTGOMERY CO.: Stockton, Harvard 45 (US), and Reverchon 505 in part (MBG). PATRICIO CO.: 5 April 1932, Tharp (T). PECOS CO.: on Marathon Road, 11 mi. s. of Fort Stockton, Cutak 1, 2 (MBG); Stockton-Sheffield, 3 May 1940, Tharp (T); Fort Stockton, 3 Nov. 1913, Wooton (US). REEVES CO.: Balmorhea Road, Tharp 7311 (T). REAGAN CO.: Best, May 1931, Groves (T). STARR CO.: Drushel 6280 (MBG); Rio Grande City, Tharp 7315 (T). UVALDE CO.: w. of Uvalde, 26 April 1931, Jones (MBG). VALVERDE CO.: Langtry, 6 Sept. 1900, Earle & Earle (NY), Orcutt 6318 (MBG); Devil River, Earle & Earle 446 (MBG, US), Tharp 3886 (PA); Del Rio, Fisher 3219 (FM), Jones 25900 (MBG); Comstock, Palmer 11055 (MBG, PA, US). WEBB CO.: between San Ignacio and Laredo, Clover 1689 (T); Laredo, Palmer 11267, and 21 March 1903, Reverchon (MBG); Greene, 7 April 1901, Eggert (MBG). COUNTY NOT DETERMINED: Del Rio to Cotulla, 40 mi. w. of Cotulla, Hanson 701 (NY, US); western Texas to El Paso, Wright 380 (G, MBG, US); between Uvalde and Del Rio, McKelvey 1894 (G).

MEXICO.—CHIHUAHUA: between San Mateo and Guasirachi, Goldman 145 (G, NY, US); Parral, 1914, Mathews (MBG); Los Reyes, about 8 mi. s. of Ciudad Jimenez, White 2117 (G).

COAHUILA: Saltillo, Adole 6349 (US), Arsène 3446 (US), Gregg 318 (G, PA), Nelson 6716 (G, US), Palmer 35 (FM, G, MBG, NY, US), Safford 1296 (US); Buena Vista, Gregg 35 (G), 749 (MBG), Wislizenus 303 (MBG); Fraile, 59 kilo. s. of Saltillo, Stanford, Retherford & Northcraft 257 (MBG, G); road from Monclova to Saltillo, 1 mi. s. of Hipolito, Johnston 7238 (G); Hipolito, between Hacienda La Rosa and Hacienda Lechuguilla, Wynd & Mueller 59 (G, MBG, NY, US); 6 mi. s. w. of Hipolito, Mueller 3012 (G); Monclova, Nelson 6154 (G, MBG), Palmer 679 (G, PA, US), Marsh 1821 (G); Hermanas, Marsh 1613 (G); Muzquiz, Marsh 523 (FM, G, T), 1050, 1114, 1142 (G); 5 mi. n. of Allende, Johnston 7009 (G); De las Neuvas a la Pena, Berlandier 2471 (G, PA); 20 mi. w. of Gloria, Drushel 9687 (US); Torreon, Juzepczuk 683 (US); Correon, Pittier 507 (US); Jaral, Pringle 9040 (G, NY, US); Jimulco, Pringle 216 (G); 11 kilo. n. e. of Jimulco, Stanford, Retherford & Northcraft 31 (G, MBG); 9 kilo. s. of Parras on Sierras Negras, Stanford, Retherford & Northcraft 159 (G, MBG); 15 kilo. w. of Concepcion del Oro, Stanford, Retherford & Northcraft 550 (G, MBG).

DURANGO: near Mapimi, Gregg 466 (MBG); near Ojo de San Bernardo, Gregg 34 (G), 509 (MBG); near Pedricena, Juzepczuk 573 (US).

NUEVO LEON: Monterrey, Abbon 6426 (US); coll. of 1828, Berlandier (G fragment), Palmer 678 (FM, G, MBG, US); s. of Nuevo Laredo on road to Monterrey, Frye & Frye 2354 (G, MBG, NY); 17 mi. s. e. of Galeana, Mexican Biological Expedition of Students of the University of Illinois 1025 (FM, G, MBG, NY); Galeana, Chase 7644 (FM, G); Rancho Resendez, Lampazos, Edwards 390 (FM, MBG, T); Sabinas Hidalgo, Kenoyer 43 (FM, MBG); 7 mi. s. of Sabinas Hidalgo, Mueller 2627 (G); 15 mi. n. of Cienega de Flores, Shreve 9428 (G); 15 mi. w. of Icamole, Safford 1266a (US); 22 mi. n. w. of Ascension, Shreve & Tinkham 9742 (G); along highway passing through Vallecillo,

Langman 1970 (PA); Laredo-Mexico highway, *Langman 2902* (PA); Laredo-Monterrey highway, *Langman 2443* (PA).

SAN LUIS POTOSI: San Luis Potosi, *Berlandier 1336* (FM photograph of TYPE, G); Charcas, *Lundell 5169* (US); near Salado, *Shreve 9356* (G, PA).

SONORA: *Schott* (FM).

TAMAULIPAS: Jaumave, *von Rosynski 305* (NY, US), *328* (FM).

ZACATECAS: 4 mi. s. of Cardona, *Johnston 7378* (G); Caopas, *Lloyd & Kirkwood 3* (MBG, US), *150* (G); near Concepcion del Oro, *Palmer 380* (FM, G, MBG, NY, US); near Calera, *Seler 552* (G).

STATE NOT DETERMINED: Valley of the Rio Grande, below Doñana, *Mexican Boundary Survey 628* in part (US).

LIST OF EXSICCATAE

The numbers in *italics* refer to the collection number, the number in parentheses to the species or variety under which the specimen is cited. The abbreviation *s. n.* indicates that the specimen is without a collector's number.

- Abbon, J. *6426* (6).
 Abrams, L. R. *14104* (1).
 Adole, L. *6349* (6).
 Allen, T. F. *s. n.* (3).
 Allen, —. *s. n.* (6).
 Anderson, Lt. A. *s. n.* (4).
 Anderson, R. C. *7749* (1).
 Archer, W. A. *7303, 7404* (4).
 Arsène, G. *3446* (6).
 Arsène, G. & Benedict. *15817* (4).
 Bailey, V. *701, 746, 1072* (4).
 Baker, C. F. *14, 106* (2).
 Ball, C. R. *1222* (5).
 Barlow, B. *s. n.* (4a).
 Barkley, F. A. & R. Blondeau. *4186* (1).
 Bartram, E. B. *294, 295, 296* (1).
 Beals, I. M. *s. n.* (4).
 Bell, W. A. *s. n.* (4a).
 Berlandier, J. L. *s. n., 1336, 2471* (6).
 Bigelow, J. M. *s. n.* (4); *2* (5).
 Bishop, Capt. F. *s. n.* (3).
 Blake, S. F. *s. n.* (4).
 Blumer, J. C. *88, 1709* (4b).
 Boll, J. *505* (5).
 Brandegee, K. *s. n.* (1); *11794* (4).
 Brass, L. J. *14203, 14330* (1).
 Bray, W. L. *416* (5); *s. n.* (6).
 Brookes, J. *s. n.* (5).
 Burnham, T. M. *291* (1).
 Carlson, J. I. *s. n.* (4a).
 Carter, A. *1420* (3).
 Chase, V. H. *7644* (6).
 Clifton, R. L. *3200* (5).
 Clokey, I. W. *5952, 7367, 7369, 8177* (1).
 Clokey, I. W. & R. G. Anderson. *7368, 8176* (1).
 Clover, E. U. *1689* (6).
 Clute, W. N. *24, 24a* (3).
 Cockerell, T. D. A. *s. n.* (4).
 Collins, D. W. *11* (4).
 Collom, R. E. *65, 479* (1).
 Cooper, J. W. *s. n.* (1).
 Cory, V. L. *17611, 2695* (4); *4666, 5322, 13478, 15195, 37520* (5); *2688, 17685* (6).
 Cory, V. L. & C. R. Ball. *1709* (5).
 Cottam, W. P. *6589* (3).
 Coues, E. & E. Palmer. *254* (1).
 Coville, F. V. & F. Funston. *292* (1).
 Cowen, J. H. *s. n., 276* (2).
 Crandall, C. S. *2995* (2).
 Creighton, H. B. *s. n.* (1).
 Cutak, L. *1, 2* (6).
 Cutler, H. C. *3135* (3).
 Darrow, R. *s. n.* (1); *s. n.* (4).
 Degener, O. *4907* (1); *4900* (3).
 Degener, O. & K. K. Park. *4411* (3).
 Demaree, D. *8031* (1); *7572, 7668, 7773* (5).
 Dewey, L. H. *s. n.* (4); *s. n.* (6).
 Dieffenderfer, F. R. *s. n.* (4).
 Drushel, J. A. *10499* (4); *6280, 9687* (6).
 Earle, F. S. *643* (4).
 Earle, F. S. & E. S. Earle. *s. n., 374* (4); *s. n., 446* (6).
 Earle, F. S. & S. M. Tracy. *42* (4).
 Eastwood, A. *3602, 5816* (3).
 Eastwood, A. & J. T. Howell. *6604* (3).
 Edwards, M. T. *390* (6).
 Eggert, H. *s. n.* (5); *s. n.* (6).
 Eggleston, W. W. *19890* (1); *17187* (3); *10650, 16323, 16538, 17285, 20399* (4); *10945* (4b).
 Evans, W. *s. n.* (4); *s. n.* (5).
 Fendler, A. *461* (4).
 Ferris, R. S. *8553* (1); *10213* (3).
 Ferris, R. S. & C. D. Duncan. *2228* (1);

- 2348, 2380, 2488 (4); 3371, 3459 (5); 2757 (6).
 Finley, I. O. 3 (5).
 Fisher, G. L. 155 (1); 3, 30, 173 (4); 3219 (6).
 Flint, W. F. *s. n.* (2).
 Fosberg, F. R. S3318 (4).
 Foster, R. C. 509 (1).
 Friese, —. *s. n.* (4).
 Frye, T. C. & E. M. Frye. 2354 (6).
 Fulton, H. J. 7359 (3).
 Gentry, H. S. 4003 (1).
 Gillespie, J. W. 8690 (1); 5263 (4).
 Gilman, M. F. 151, 215 (1).
 Goddard, D. R. 810 (4).
 Goldman, E. A. 2893 (3); 145 (6).
 Goldstein, G. W. *s. n.* (4).
 Goodding, L. N. 752 (1).
 Gordon, A. *s. n.* (5).
 Gorder, C. van. 49 (5).
 Graham, H. W. *s. n.* (1).
 Grassel, C. O. 26 (4).
 Graves, H. *s. n.* (5).
 Gray, A. *s. n.* (3).
 Greene, E. L. *s. n.* (1); *s. n.* (4).
 Gregg, J. 34, 35, 318, 466, 509, 749 (6).
 Griffiths, D. 2020 (1); 5173, 5741 (4).
 Groves, H. *s. n.* (6).
 Hanson, H. C. *s. n.*, A55 (3); 608, 650 (4a); 701 (6).
 Harris, J. A. C1476 (1).
 Harrison, C. H. & T. H. Kearney. 8667 (1).
 Hartman, C. V. 726, 807 (4).
 Harvey, D. R. 518 (1).
 Havard, V. 45 (6).
 Hayes, S. 469 (4); *s. n.* (5).
 Heary, —. *s. n.* (5).
 Heller, A. A. 15777 (3).
 Heller, A. A. & E. G. Heller. 3739 (4).
 Herrick, C. L. 651 (4); 643 (4a).
 Herrick, C. J. & J. Herrick. 108, 137 (4).
 Hilzinger, G. *s. n.* (1).
 Hinckley, L. C. *s. n.*, 652 (4).
 Hitchcock, A. E. *s. n.*, 51, 71 (3).
 Hitchcock, A. S. *s. n.* (3); *s. n.*, 741 (5).
 Hitchcock, C. L., R. V. Rethke, & R. Van Raadshooven. 4276 (4).
 Hoaglund, P. 7303, 7313 (6).
 Holstein, G. W. *s. n.* (5).
 Holzinger, J. M. *s. n.* (4).
 Hough, W. 115 (4).
 Howell, H. A. 51, 52 (5).
 Huber, W. *s. n.* (4).
 Hubricht, L., C. Shoop & D. B. Heinze. *s. n.* (4); B1389 (5).
 Huffmann, W. T. *s. n.* (3); *s. n.* (4); *s. n.* (4a).
 Innes, R. R. & B. Moon. 1004, 1061 (5); 1168 (6).
 Innes, R. R. & B. H. Warnock. 501 (4a).
 James, T. P. *s. n.* (4).
 Johnson, F. W. *s. n.* (1); *s. n.* (4).
 Johnston, I. M. 8183, 8437 (4); 7009, 7238, 7378 (6).
 Johnston, I. M. & C. H. Muller. 67, 760, 1382 (4).
 Jones, M. E. *s. n.*, 3891, 25940 (1); 5474, 5296 in part (2); 4038, 5291i, 6050a, 5296 in part, 5696e (3); 285, 3718, 25943 (4a); *s. n.*, 25900, 36415 (6).
 Juzepczuk, S. 573, 683 (6).
 Kearney, T. H. & R. H. Peebles. 12741 (3).
 Keck, D. D. 4147 (1).
 Kellerman, W. A. *s. n.* (5).
 Kennedy, P. B. 1127 (1).
 Kenoyer, L. A. 43 (6).
 Knowlton, F. H. 182, 272 (3).
 Langman, I. K. 1970, 2443, 2902 (6).
 La Rivers, I. & N. F. Hancock. 294 (1).
 Leiberg, J. B. 5624 (3).
 Lemmon Herb. 46 (1); *s. n.* (4b).
 Le Sueur, H. 54 (4).
 Letterman, G. W. 25 (5).
 Lloyd, F. E. & J. E. Kirkwood. 3, 150 (6).
 Long, H. C. *s. n.* (2).
 Lundell, C. L. 5169 (6).
 MacDougal, D. T. 229 (3).
 McKelvey, S. D. 4454 (3); 1974, 1980 (4a); 1894 (6).
 Maguire, B. & H. L. Blood. 4498 (1).
 Maguire, B., R. Maguire & H. L. Maguire. 5060, 5061 (1).
 Marsh, C. C. *s. n.* (3).
 Marsh, E. G. 79, 901, 1233, 1340, 1522 (4); 523, 1050, 1114, 1142, 1613, 1821 (6).
 Mathews, E. O. *s. n.* (6).
 Mearns, E. A. 253, 1525 (4); 2186 (4b).
 Meebold, —. 22544 (4a).
 Metcalfe, J. K. *s. n.* (4).
 Metcalfe, O. B. 124, 648 (4); 1144 (4b).
 Mexican Biological Expedition of Students of the University of Illinois. 1025 (6).
 Mexican Boundary survey. 628 in part (4); 629 (4a); 628 in part (6).
 Moore, J. A. & J. A. Steyermark. 3114 (6).
 Mueller, C. H. 8231 (4); 2627, 3012 (6).
 Mulford, I. A. 111 (4); 941 (4b).
 Munz, P. A. 13897 (1).

- Nelson, A. 6319, 6441, 11671 (4); 6154, 6716 (6).
 Nelson, A. & R. A. Nelson. 1519, 1535 (1); 2179 (4).
 Orcutt, C. R. 6028 (5); 6318 (6).
 Osterhout, G. E. 2127 (2).
 Palmer, E. 140, 246, 538 (1); 246½ (3); 164 (4a); 35, 380, 678, 679 (6).
 Palmer, E. J. 32083, 34216 (4); 11088, 12472, 12520, 13050, 14049, 33542, 34573, 41863 (5); 11055, 11267, 30590A (6).
 Parish, W. F. 111 (1).
 Parish, S. B. 10264, 10285 (1).
 Parry, C. C. s. n. (3).
 Payson, E. 658 (2).
 Peebles, R. H. 9539, 13332 (3).
 Peebles, R. H., G. H. Harrison & T. H. Kearney. s. n., 1279 (1).
 Pilsbry, H. A. s. n. (3); s. n. (4); s. n. (4b); s. n. (5).
 Pittier, H. 507 (6).
 Plank, E. N. s. n. (4).
 Pringle, C. G. s. n., 9845, 13755 (1); 9954 (4); 71, 71½ (4a); 216, 9040 (6).
 Purpus, C. A. 6125 (1); 183 (2); s. n. (3).
 Reed, E. L. 3094, 3408, 3799 (5); 1811 (6).
 Reed, E. L. & D. Demaree. 7636 (5).
 Rehn, J. A. G. & H. L. Viereck. s. n. (4a).
 Reverchon, J. s. n., 505 in part, 3328, 3328A (5); s. n., 505 in part (6).
 Rollins, R. C. 1578, 1970, 2141, 2155 (2).
 Rollins, R. C. & T. S. Chambers. 2440 (3); 2418 (4); 2757 (6).
 Rose, J. N. 1193 (4).
 Rose, L. S. 40083 (1).
 Rosynski, H. W. von. 305, 328 (6).
 Rothrock, J. T. 82, 463 (4).
 Rusby, H. H. 657, 4734 (3); 175½ (4).
 Ruth, A. 1283 (5).
 Rydberg, P. A. & R. Imler. 716, 796a, 1120 (5).
 Safford, W. E. 1266a, 1296 (6).
 Saunders, D. 405 (2).
 Schott, A. III 91 (1); s. n. (6).
 Schulz, —. 38-39 (5); 3001 (6).
 Schrenk, H. von. 37, 42 (6).
 Seler, E. 552 (6).
 Shepard, M. s. n. (5).
 Sherff, E. E. s. n. (1).
 Shreve, F. 9356, 9428 (6).
 Shreve, F. & E. R. Tinkham. 9742 (6).
 Siler, A. S. s. n. (3).
 Smith, B. H. s. n. (4).
 Smith, J. G. 25 (4).
 Smyth, B. B. 140 (5).
 Sperry, O. E. 250 (4); 1709 (4a); T346, 743 (6).
 Standley, P. C. s. n., 6445, 40359 (4).
 Stanford, L. R., K. L. Retherford & R. D. Northcraft. 31, 159, 257, 550 (6).
 Stearns, E. s. n., 384 (4).
 Stevens, G. W. 258½, 593, 715, 973, 1052, 1637 (5).
 Stewart, R. M. s. n., 544, 801, 884, 1273, 1485, 1572, 2161 (4).
 Stokes, S. G. s. n. (2).
 Stone, F. M. 60 (1); 276 (3).
 Stone, W. 184 (4).
 Swift, —. s. n. (5).
 Tharp, B. C. s. n. (1); s. n., 286 (5); s. n., 3886, 7311, 7315 (6).
 Thompson, A. P. s. n. (3).
 Thornber, J. J. 402 (1).
 Thurber, G. 76 (4).
 Toumey, J. W. s. n., 639a, 639b, 639c (1); 638 (3).
 Townsend, C. H. T. & C. M. Barber. 364 (4).
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HEISER—MONOGRAPH OF PSILOSTROPHE

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MAIZ REVENTADOR¹

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A remarkable kind of maize discovered in western Mexico by Dr. Isabel Kelly seems not to be known to maize experts, nor to have received any published mention, even of the most casual sort. This is certainly owing in part to the fact that with maize, as with other matters, western Mexico tends to be ignored. It may also reflect the fact that even in most of the area where we have studied this variety, a stranger interested in maize might travel for some time without meeting it in the market-place, the granary, or growing in the field.

In most of that area this maize is known as "*maíz reventador*" (literally "exploder corn", i. e. popcorn), so we shall refer to it by that name though in Jiquilpan and elsewhere in Michoacán it is known (if at all) as "*maíz rosquera*", and this name is current in parts of Jalisco as well. In the region around Purificación, Jalisco, the name "*reventador*" is used, though "*pipitillo*" is also employed, perhaps due to local hybridization with an imported variety of that name (see below). While *maíz reventador* is commonly used as a popcorn it is a completely different thing from the narrow-grained rice popcorns of central Mexico and bears only a general resemblance to the pearl popcorns of commerce.

Maíz reventador is small-grained, small-cobbed, flinty and undented (see fig. 1, table I, and pls. 15 and 16). It is 12–16-rowed, with grains 6–7 mm. wide and about as high as they are wide. It is characteristically pure white, though red pericarp is well established in some localities. While yellow grains or occasionally all yellow ears are seen, all those which we have submitted to progeny tests showed obvious signs of having been crossed with other kinds of

¹ Much of the work reported in this paper was carried out while the author was a Fellow of the Guggenheim Foundation. Facilities for progeny tests were made available by the California Institute of Technology and by the Blandy Experimental Farm of the University of Virginia. Grateful acknowledgment is made to these institutions, to Prof. Carl Sauer, who provided the material for the initial study, and to Dr. Isabel Kelly, who made most of the actual collections and supplied much critical information. As it stands, the paper is very largely due to her help and advice though she is in no way responsible for its imperfections.

TABLE I
EAR AND KERNEL CHARACTERISTICS FOR COLLECTIONS OF MAIZ REPENTADOR AND MAIZ CHAPOLOTE

| Collection locality | State | Number ears measured | Mid-ear width* | Ear-stalk diameter* | Kernel width* | Kernel thickness* | Row number | Color |
|---------------------|-----------|----------------------|----------------|---------------------|---------------|-------------------|------------|--------------------------|
| Chachahuatlán | Jalisco | 25 | 2.8-3.2-3.7 | .7-1.0-1.3 | .4-7-1.0 | .3-3-4 | 10-14-16 | White |
| Jiquilpan | Michoacán | 25 | 2.5-3.1-3.6 | .5-1.0-1.3 | .5-7-1.0 | .3-3-4 | 10-14-16 | White |
| Coahuacán | Michoacán | 1 | 3.3 | 1.0 | .7 | .3 | 14 | White |
| La Huerta | Jalisco | 2 | 3.1 | 1.2 | .5-7 | .3-4 | 14-16 | White |
| Tenamaxtlán | Jalisco | 3 | 2.5-2.9-3.1 | .7-9-1.0 | .6-7-7 | .3-3-4 | 10-14-14 | White (one red pericarp) |
| Avotitlán | Jalisco | 4 | 2.9-3.1-3.5 | .9-1.1-1.5 | .7-7-8 | .3-3-4 | 12-14-16 | White |
| Culiacán | Sinaloa | 2 | 2.7 | .8-9 | .7-8 | .3-4 | 10-12 | Tan pericarp |

*Where three numbers are given the first is the lowest value in the collection; the next is the average (median); and the last is the highest. All measurements are in centimeters.

maize (see below). The husks are extremely tight and longitudinal compression lines can be seen running more or less the length of the ear, across the face of the kernels. The kernels are in straight rows, but the pairing of the rows is not evident, and since successive kernels in any row usually are of different shapes and frequently of different sizes they may be described as "tesselated" in contradistinction to those kinds of maize in which successive kernels in a row tend to be mechanically uniform in size and in shape.

The plant descriptions which follow are from end-season plants examined at Chachahuatlán, near Tuxcacuesco, Jalisco, Mexico, and from progeny tests grown at the Blandy Experimental Farm of the University of Virginia and at the experimental fields of the California Institute of Technology at Arcadia, California. It is known that many of the characters discussed below are affected by length of day, and it is probable that other factors such as night temperature are also important. This is particularly true of the date of maturing and number of tillers, two characters which are notoriously affected by place and time of planting.

Both at the Blandy Farm and at Cal. Tech. the plants of *maíz reventador* were extreme in their vegetative characters. They had narrower leaves with deeper channels above the midrib and with heavier midribs than any other varieties grown with them or studied previously at these laboratories. They bore more tillers, which were less differentiated from the main stalk, and they were later to mature. In Virginia they were not able to tassel before the growing season was stopped by frost, though other Jalisco varieties managed to tassel if not to set seed, and maize from the highlands of Michoacán was only a little slower to mature than the local Virginia corn. In California they were later-seasoned than anything else in our cultures, much later than corn from Michoacán and a month later than sweet corn, "*maíz dulce*", from Jalisco.¹ Furthermore, the yellow-grained *maíz reventador*, which was most certainly the result of crossing between white *reventador* and other varieties, was the earliest of these popcorns to mature, some of its plants being only a week later than the Jalisco sweet corns. In Jalisco most maize is planted so late in the season, due to the dry winter and spring, that tillering is discouraged. However, from the results reported above we know that, given the proper conditions, *maíz reventador* is later-seasoned and has more tillers than any other maize which we have grown in our extensive tests.

The plant color of *maíz reventador* was also extreme, though similar to that of varieties grown by the Papago Indians and their relatives. There was no color on the upper leaves, but more or less of a dark mahogany-red was apparent on the exposed parts of the stem. On the leaves below the node bearing the ear there was no color on the blade except around the auricle, which was quite deeply marked with red on some plants. The sheaths of the lower leaves were evenly (and often brightly) colored with a clear red along the veins, even when they

¹ Kelly, Isabel, and Edgar Anderson. Sweet corn in Jalisco. *Ann. Mo. Bot. Gard.* 30:405-412. 1943.

were not exposed to strong light. On some plants there was a slight deposit of color between the veins, but even on these plants the superficial aspect was that of red veins on a green background. The silks were uniformly green or a light sun-red that bleached out in the sun and could only be detected on cloudy days. The anthers were green or a very pale sun-red. There was a considerable and variable deposit of dull red on the glumes of the tassel. Five of the progeny tests of collected ears showed a heavy marking of red at the base of the glume (glume bar); one showed only a faint glume bar.

The tassels were long, slender, and wiry with small to average spikelets but very long branches. The lower internodes of the tassel were often extremely long, producing tassels of large size and low density. Most of the plants had 15 to 30 branches but there were a few with "ramosa-type" tassels which lacked a developed central spike and bore many short branches, decreasing in size towards the apex of the tassel.

The plants from the yellow-kerneled ears were similar in all the above characteristics, but were more variable and possessed numerous features characteristic of other kinds of Mexican maize. Some of them had bright red silks and tassels; most of them had a strong development of interveinal color on the sheaths of the upper leaves, and their tassel branch number, while extremely variable, was smaller (table II). As mentioned above, they were earlier-seasoned and had fewer tillers. All of these results would be expected if they were crosses between white *maíz reventador* and yellow Jaliscoan sweet corns. Mr. Raymond Baker, who used one of these yellow ears in a cross, reports that sweet kernels segregated out in the second generation, practically proving this assumption.

Most of the variability in our collections of *maíz reventador* seems to be due to crossing with other kinds of maize, such as that just described with *maíz dulce*. Thanks to the interest of Sr. F. Vargas Tentory, we received maize collections from three forest clearings in the Coalcomán area of Michoacán (1) on Map 1). A variety very similar, if not identical, to *maíz reventador* was present in all three clearings, though in two of them it sometimes had a bright red pericarp. In two of the collections there were many obvious intermediates between *maíz reventador* and larger-grained varieties. Similar collections have recently been received from the coast of Michoacán.

Resemblances.—The only variety closely resembling *maíz reventador* which has come to our notice is a series of ears presented by Ing. Taboada of the Dirección General, Secretaría de Agricultura y Fomento, to whom we are indebted for these and other favors. The ears presented by Ing. Taboada came from Culiacán, Sinaloa (14) Map 1), where they are known as *maíz chapotc*. They are quite similar to *maíz reventador* except that they look even more primitive and have a dark tan pericarp. The plants differ in being much shorter-seasoned. *Maíz reventador* is of particular interest because it is so much like a kind used in western Mexico in the Colonial period (see below). Two archeological occurrences are known, both excavated by Dr. Isabel Kelly, one at Paso Real, Jalisco (5)

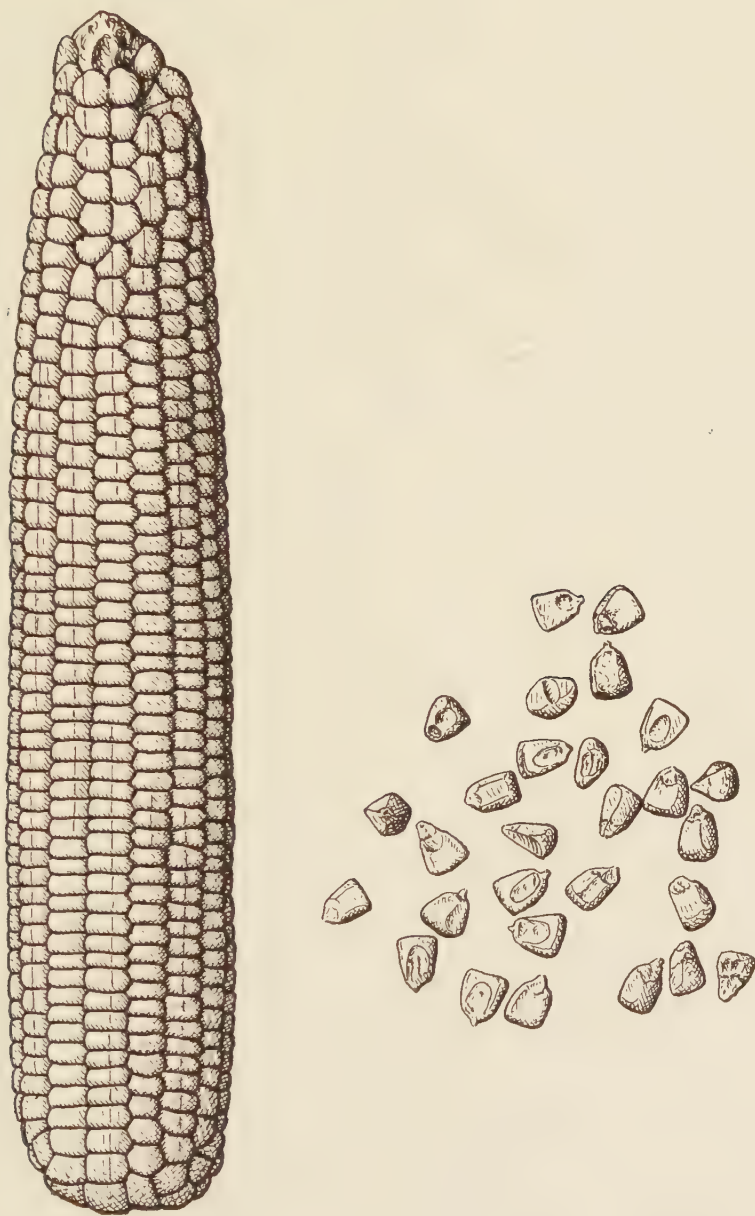


Fig. 1. Ear of *Maíz reventador* from Chachahuatlán, Jalisco, and shelled kernels from the same. Natural size.



Map 1: Distribution of *maíz reventador*: Solid black dots, regions where it is *not* grown and is apparently unknown; open circles, localities where *maíz reventador* or a very similar variety was collected or from which a similar, if not identical, variety is known from archeological investigation or historical documents. See the text (pages 309–311) for further details.

Map 1), on the Rio Armeria, downstream from Tuxcacuesco, and the other from Culiacán, Sinaloa (14). Both are only charred fragments of cobs but these are large enough for us to estimate kernel-size, cob-size, tessellation, and row number. If these charred fragments did not belong to *maíz reventador*, as here described, they must have belonged to some closely related small-cobbed, small-grained variety.

A detailed description of the fragments from Paso Real will be found in an appendix to Dr. Kelly's report on that area. Those from Culiacán were not received until that report was in press and are described here to put the facts on record.

As received for examination from the Museum of Anthropology of the University of California the material consisted of several carbonized cob fragments without kernels. The box bore the specimen number 3-6090, and Mr. Gifford's accompanying letter stated that

it was Dr. Kelly's original number 46, from Culiacán, Sinaloa, Trench 2.

The largest fragment was an entire cross-section of a small cob, apparently from near the base. Since one of the smaller fragments was also basal, apparently at least two cobs were represented in the sample. The fragments were conspicuous by the small size of the spaces for the kernels, being slightly smaller than the smallest previously examined in this laboratory (Haury's material from Ventana Cave). The mid-cob width was 1.5 cm., the cob-kernel width was 2 mm. and the cob-kernel thickness was 2.8 mm. giving a cob-kernel area of 5.6 sq. mm.

The largest fragment is somewhat imperfect on one side and the row number cannot be absolutely determined. It is at least 14 and it might possibly be 18. There is no indication of the ear being elliptical, as in much primitive maize, and from the fragments one would judge the ears to have been cylindrical rather than tapering.

As a whole, the material is similar to that discovered by Dr. Kelly at Paso Real. It apparently was a small-grained flint, probably of the same general type as the small-grained popcorns or flints which are still to be found in western Mexico.

In a number of ways *maíz reventador* is quite similar to the remarkable maize grown by the Pima and Papago Indians, resembling it in plant color, narrow cobs, tessellated seeds, well-developed tillers, and prominent husk striations.

Most of the peculiarities of *maíz reventador* are to be found in an even more exaggerated degree in teosinte (*Euchlaena mexicana*). This is true of the narrow leaves, the slender stems, the tough roots, the late season, the wiry tassel, and the small seeds. The kernels of *maíz chapolote* from Culiacán are even of the same dark brown as teosinte. Furthermore, this variety has large knobs on every chromosome except No. 10. It would seem as if these western Mexican varieties represent a maximum introgression of teosinte. If so, this must have occurred at some time in the past. While teosinte is not unknown in western Mexico it is now a rarity in the fields where we have studied *maíz reventador*.

In a very general sort of way *maíz reventador* is somewhat similar to the maize varieties commonly grown in Jalisco. All of these varieties (known locally by such names as *maíz criollo*, *maíz blanco*, *maíz colimato*, *maíz humeado*, etc.) have a strong tendency to narrow, irregularly tapering ears, strongly appressed at the base, and to husk striations on the kernels (pl. 16, below). They have the general appearance of crosses between *maíz reventador* and other kinds of corn. To use a phrase employed by certain anthropologists, they probably contain *maíz reventador* "in solution." This assumption is at least partially confirmed when the variation in these varieties is examined plant by plant. If they have indeed resulted from crosses between *maíz reventador* and other kinds of maize, then the amount of *maíz reventador* germ-plasm (as well as its kind) should vary greatly from plant to plant, and we might expect to find occasional plants which have the maximum amount possible in that population ("reëmergents," in the language of the physical anthropologists). Such plants should be very similar to *maíz reventador*. This is actually the case. In almost any corn crib in Autlán or Guadalajara or Ameca one will find occasional ears which show a strong resemblance to *maíz reventador*, much stronger than that of most Jaliscan maize. Much more rarely one may even come across a single ear which is almost within range of variation of *maíz reventador* itself.

TABLE II
TASSEL CHARACTERISTICS OF PLANTS GROWN IN THE UNITED STATES FROM COLLECTIONS OF MAIZ REVENTADOR

| Collection | Locality | State | Plants raised to maturity | Number tassel branches* | Glume length in mm. | Glume bar | % condensed internodes | % sub sessile spikelets |
|---------------------------------|-------------|---------|---------------------------|-------------------------|---------------------|-----------|------------------------|-------------------------|
| Ears with small white kernels | | | | | | | | |
| K. 1 | Sayula | Jalisco | 6 | 13-21-28 | 9 | Heavy | 0 | 0 |
| K. 2 | Talpa | Jalisco | 7 | 15-19-36 | 9 | Heavy | 0 | 0 |
| K. 3 | Mascota | Jalisco | 5 | 18-26-33† | 10 | Heavy | 0 | 0 |
| Sa. 22 | Ayotitlán | Jalisco | 4 | 23-26-29 | 10 | Faint | 0 | 0 |
| Ears with larger yellow kernels | | | | | | | | |
| K. 4 | Talpa | Jalisco | 5 | 12-13-29 | 12 | Heavy | 10 | 100 |
| Sa. 11 | Tenamaxtlán | Jalisco | 5 | 15-23-28 | 11 | Heavy | 40 | 40 |

*In the figures for number of tassel branches the middle represents the average (median) value; the others, the lowest and highest values.
†Excluding one plant with *ramosa* type tassel.

Some of our collections demonstrate the way in which *maíz reventador* tends to become incorporated with new varieties introduced into the region where it is grown. From the Purificación area, for instance, we have collections from Villa Vieja ((7) Map 1) and from La Huerta. They demonstrate an apparent blending of *reventador* and a widely grown Mexican variety known as *pipitillo*. From Villa Vieja we have three ears which were being grown under the name of *pipitillo* and were said to be the common corn of that region. As a whole, they look more like *reventador* than like *pipitillo* as that name is commonly applied in other parts of Mexico (Guanajuato, Michoacán, Mexico, Morélos, etc.). However, as compared with pure *reventador* they are larger-grained, larger-cobbed, and with proportionately longer kernels. On closer inspection one of the ears (pl. 16, extreme left, below) is enough like *pipitillo* so that it might pass under that name in a region such as the Los Altos zone of Jalisco where *pipitillo* is not as extreme in type as it is around Mexico City. It is not only outstanding for the characters enumerated above but it has kernels more or less dented; it has a conspicuous capping of starch and some of the kernels show a slight tendency to pointing (all of these being attributes of *pipitillo*). It would seem as if a genuine *pipitillo*, once introduced into this region, is now so swamped by repeated contamination with the local *reventador* that there are only traces of its original characteristics. This suspicion is confirmed by the collection from La Huerta (pl. 16, above) in the same general region. This consists of four ears, two of which are practically pure *reventador* and two of which have colored aleurone and slightly larger seeds. Significantly, they were identified locally as "*pipitillo (reventador)*".

It seems not unlikely therefore that *maíz reventador*, or at least some very similar variety or varieties, is the foundation stock for the maize of western Mexico and the reason why the maize of that region is so distinctive as a whole. This conclusion is in accord with the archeological information reported above and with the evidence from a colonial document reported in the following section on distribution.

Distribution.—The known distribution of *maíz reventador* (see map 1) lends further weight to the above assumptions. From our own collections we know it to be widespread in western Jalisco, with collections from the Jalisco plateau and from its southwesterly slopes and fringes. Specimens have been collected at Tenamaxtlán (10)¹, Ayutla (10), Mascota (9), Talpa (8), El Limón (5), and Sayula (6). It is reported by several reliable informants from Ameca (11). We also have collections from Chachahuatlán (5) and Tuxcacuesco (municipality of Tuxcacuesco) (5), from Las Canoas and Ayotitlán (municipality of Autlán) (4), and from Villa Vieja (7), La Huerta and Pueblo Nuevo (Cuautitlán of older maps), all from the municipality of La Purificación as of 1943 (we are informed that this area is being redistricted). We have specimens from the old town of Tlajomulco (12) which are not quite typical and seem to have been mixed with modern commercial pearl popcorn. We have shelled corn sent from

¹ Numbers in parentheses are from Map 1.

Tepic (13), Nayarit, and which was said to be grown near by. We also have specimens from Jiquilpan, Michoacán (2), on the border of Jalisco, and an unusually reliable informant reports it as fairly common in those parts of Michoacán (3) which are adjacent to LaBarca, Jalisco.

Unfortunately, it is not possible to be as definite about regions where it certainly does not occur (or at least did not occur). In most of the areas studied its occurrence is now so casual that it can be found only after persistent search. In S. P. Tlaquepaque, near Guadalajara, it was not grown during 1943 but it is occasionally grown there, and within the memory of many inhabitants it was regularly grown by a few families. We have not collected it in the Los Altos zone of Jalisco, and several informants from that area did not recognize the name or sample cobs. In Guanajuato we are on firmer ground because of the extensive collections made by Dr. E. Limón of the Campo Agrícola Experimental at León. He did not know it and nothing like it was represented in his collections. We are convinced that it does not now occur and has not recently been grown in the highlands of Michoacán (Cherán, San Lorenzo, Pátzcuaro, Uruapan) or in the region of intensive maize culture around Mexico City. In the collections of the Dirección General de Agricultura y Fomento at San Jacinto there are no ears even remotely like it from any of these regions and the specimen ears which we carried were viewed with equal astonishment by farmers, dealers, and agricultural experts. (In Jalisco, on the other hand, they were usually recognized, and the peculiar properties of the variety were described even in those towns where none was being grown in the current year.)

In addition to its general resemblance to west-coast maize one reference suggests that *maíz reventador* was formerly widely distributed northward. In the Biblioteca del Estado in Guadalajara there is a manuscript copy¹ of the 1776 Relación of (San Miguel de) Sahuaripa, (15) map 1, in Sonora, which describes a *maíz "reventador"* with small white grains and says that in the form of *pinole* it was common provender of the area².

We have several times referred to the casual occurrence of *maíz reventador* at present. It may be well to present in detail some of the actual facts on which this statement is based. In Tuxcacuesco (5) it is grown by a single family who pops it and sells popcorn balls locally. At Chachahuatlán several families grow a little of it, usually only one row or part of a row in their *milpa* (yellow *maíz dulce* is often grown in the same incidental way in an adjoining row which accounts for part of the yellow kernels). At Ameca (11) several reliable informants report it as being grown in this same way by a very few families. In

¹ Manuscript No. 50, T. III.

² "Ay reventador que llaman; pequeno el grano, y blanco este porque abunda para pinole que lo asen tostando dicho Maíz y moliendo,¹⁰ y es el Bastimento corriente de la tierra, el qual toman batido en agua fria, lo reserban solo para esto" . . . There is (the kind) called popcorn, with little white grains, for this is abundant. They make pinole of it, toasting the aforesaid maize and grinding it up and it is the regular food stuff of the land, being eaten stirred up in cold water; they reserve it [popcorn] for this alone. [Spelling and punctuation somewhat modernized.]

Jiquilpan, Michoacán (2), two families make a regular practice of selling popcorn balls in the local markets and on the street outside their houses. They grow a little themselves and occasionally buy additional ears. In Tlajomulco (12), in 1943, it was grown by only one family who had 15 or 20 plants along one edge of their corn field.

In questioning informants as to where it might be obtained we have often (Ameca is one exception) met with the statement that more of it was being grown up in the hills ("en el cerro"). Questions as to why it was more frequent in the hills met with a variety of answers ("more water", "better soil", "better drainage", etc.). We suspect that if it is indeed commoner in the hills, as has been so frequently reported, it is there because it is an ancient kind of maize and like many other ancient things it survives longest in out-of-the-way places.

Uses.—Maíz *reventador* is used at the present time for popcorn and for *pinole*, though the latter is made from other varieties of maize as well.¹ Sometimes the popcorn is sold as loose grains, with or without sugar or salt, but more frequently it is made into balls by the addition of *panocha* (crude brown sugar) syrup. These are variously known as *chivitas*, *palomitas*, and *rosqueras* (the names also used in other parts of Mexico when other kinds of maize are used for popping). In Jiquilpan, Michoacán, the unpopped grains are used in the manufacture of thin sweet cakes, locally known as *ponteduro*. This confection can be made with a variety of materials and is usually prepared as loose, sugar-coated grains.¹

Directly, *maíz reventador* would seem to be of very limited economic importance. As a popcorn it seems to be inferior to modern commercial varieties. Indirectly, however, it may be of great potential importance. Modern maize breeding is now at the point where it is beginning to improve commercial varieties by planned crosses to bring in desirable characters. For such a program *maíz reventador* has a great deal to offer. It has tough stalks and a tough strong root system. The hard-surfaced leaves and stems are resistant to insect attack and it has tight, tough husks which protect the ear. Some of these qualities may prove useful in creating the maize of the future.

SUMMARY

1. Though previously unmentioned in maize literature, *maíz reventador* is widely, if not commonly, grown in western Mexico. Its prevalence in out-of-the-way places, as well as its close resemblance to the charred remains of prehistoric maize from western Mexico, suggests that it was once a staple crop there. Further confirmation for this suggestion is given by the general resemblances of commercial varieties in the west of Mexico to *maíz reventador*, by the appearance of occasional plants which resemble it even more closely, and by the description of the same or a similar maize in a manuscript of 1776.

¹ Kelly and Anderson. *loc. cit.*

2. *Maíz reventador* is described in detail. It is outstandingly slender, in cob, leaf and stem; it has tough, strong leaves, stems, and roots. Plant color, when strongly developed, is chiefly along the veins of the leaves rather than between them.

3. It is used locally for confections (*pinole* and popcorn balls).

4. Several of its outstanding characteristics make it important in modern maize-breeding programs.

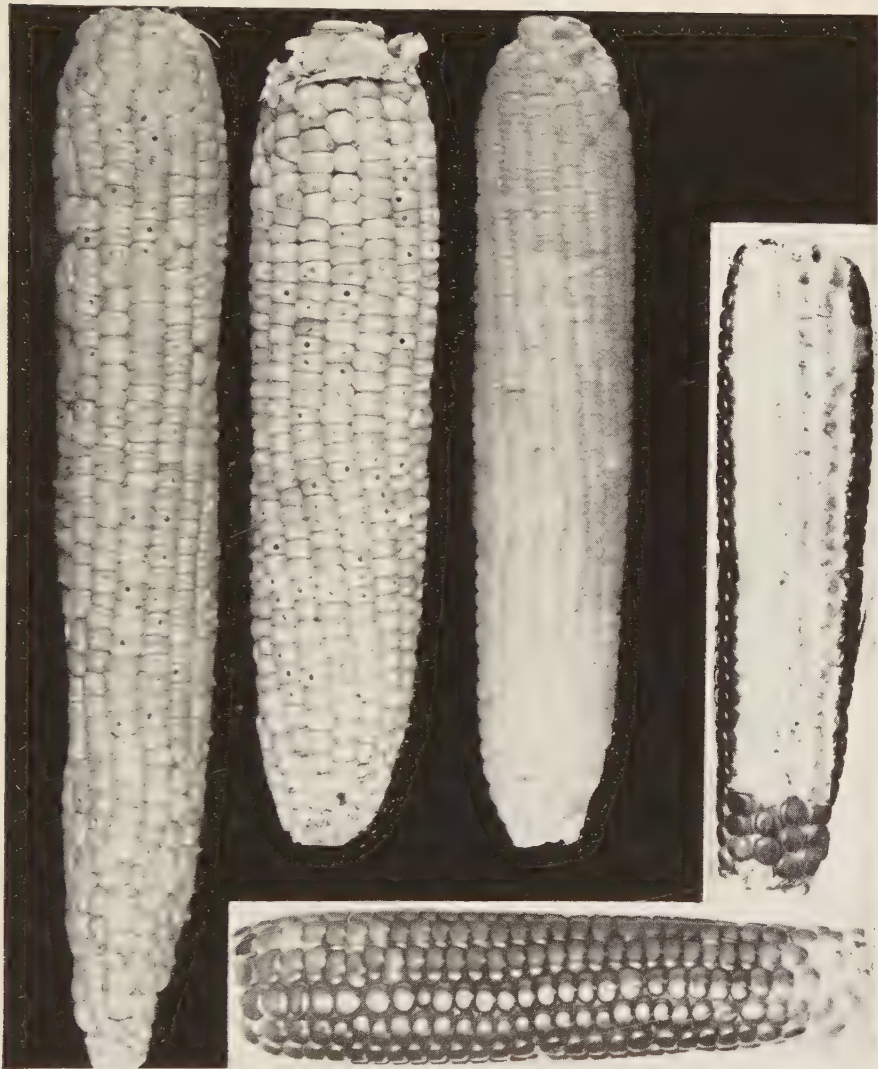
EXPLANATION OF PLATE

PLATE 15

Three ears of *maíz reventador* and two of *maíz chapolote* (approximately natural size).

Upper left: two ears of *maíz reventador* from Tuxcacuesco, Jalisco (badly damaged by insects), and one from Sayula, Jalisco. Photographs courtesy of the Anthropological Museum of the University of California.

Lower right: two ears of *maíz chapolote* from an *ejido* near Culiacán, Sinaloa, Mexico.



ANDERSON—MAIZ REVENTADOR

EXPLANATION OF PLATE

PLATE 16

Maíz reventador and other varieties of maize from Jalisco which show probable mixture with it. All ears approximately one-half natural size.

Above, left to right: *maíz reventador* from La Huerta (3 ears), Las Canoas, and Tenamaxtlán (2 ears). The ears from La Huerta were received under the names of *pipitillo* (*reventador*), *blanco* and *negro*.

Below, left: Three ears of *maíz pipitillo* from Villa Vieja which are so extensively mixed with *maíz reventador* that only the ear at the extreme left bears any noticeable resemblance to the varieties known by that name in the districts around Guadalajara, Mexico City, or León. See text, page 309.

Below, right: Two ears of other varieties from Jalisco, demonstrating the general resemblance to *maíz reventador* which characterizes the maize of that region. Next to last: *maíz tomateco*, La Huerta. Extreme right: *maíz olatillo*, Ayutla.



ANDERSON—MAIZ REVENTADOR

CYTOLOGICAL OBSERVATIONS ON *TRIPSACUM DACTYLOIDES*

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Taxonomic work on *Tripsacum*¹ has indicated that *T. dactyloides* is a very complex species. It is composed of at least five different entities, one of which grows in an isolated area in western Texas and has been recognized taxonomically as *T. dactyloides* var. *occidentale* (loc. cit). Aside from this variety, *T. dactyloides* extends from central Texas and northern Kansas eastward to Connecticut and Florida (Map 1). Cytologically, *T. dactyloides* is a polyploid complex and has some races with 18 pairs of chromosomes and others with 36. The cytological work reported below extends the known range of one diploid race into Missouri and Arkansas and suggests that *T. dactyloides* may be exclusively tetraploid along the eastern seaboard.

Materials and Methods.—At the beginning of the project an earnest attempt was made to cultivate the Mexican and Guatemalan species of *Tripsacum* along with a comprehensive collection of the various forms of *T. dactyloides*. After three years of partial success this had to be abandoned as too costly in time and effort. None of these species are winter-hardy in St. Louis, even with careful attention, and even the southern Texas strains of *T. dactyloides* get gradually weaker, and a few die each winter. As a greenhouse plant *Tripsacum* does well in St. Louis during the winter, but it is difficult to bring through the long, hot summer. The collection was kept in fair condition for two years by transplanting to the breeding plot every spring and then putting the plants back into the greenhouse in September. However, when they are treated this way they do not have a regular flowering period, and some of them do not flower at all. A project of this sort could be carried out more efficiently at some such experiment station as La Jolla, California, or College Station, Texas, where the exotic species of the genus are easily grown out of doors. Since *Tripsacum* is a close relative of maize and may even be involved in the history of our cultivated varieties,² such a project would seem to be of fundamental importance.

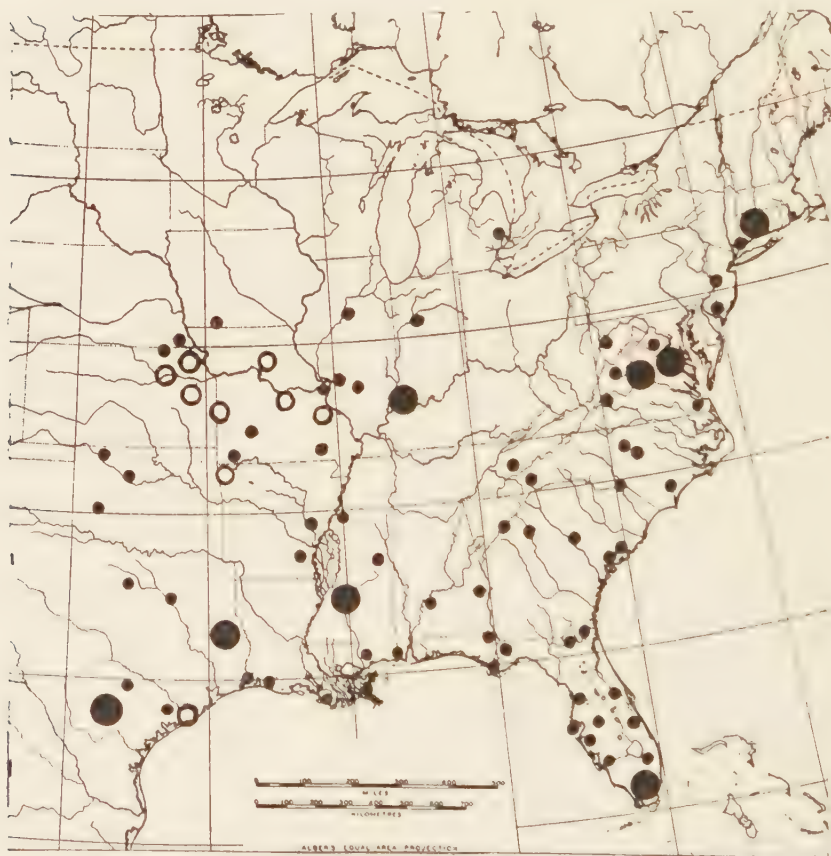
From the more northerly part of its range *Tripsacum dactyloides* was readily grown from seeds or as transplants. Seedlings grew best when planted out of doors and brought in after several weeks of cold weather. Planted out the following spring, they gave good-sized plants by the second summer. In transplanting specimens from the wild, early fall was found to be the most effective time of year and preferable to summer, late fall, or spring. The plants grew well when

¹ Cutler, Hugh C., and Edgar Anderson. A preliminary survey of the genus *Tripsacum*. *Ann. Mo. Bot. Gard.* 28:249-269. 1941.

² Mangelsdorf, Paul C., and R. G. Reeves. The origin of maize. *Nat. Acad. Sci., Proc.* 24:303-312. 1939.

once established, and required only an occasional weeding to keep them in good condition. The following collections have been examined cytologically:

| | | |
|--------------------------|--|----------|
| <i>Deam</i> | Collected by Dr. C. C. Deam 7 miles east of Lincoln City, Spencer Co., Ind. | $n = 36$ |
| <i>Dederick</i> | Plants collected by Leslie Hubricht along stream near Dederick, Vernon Co., Mo. | $n = 18$ |
| <i>Fourche a du Clos</i> | Plants collected 3 miles north of Bloomsdale, Ste. Genevieve Co., Mo., by Leslie Hubricht. | $n = 18$ |
| <i>Rivanna</i> | Plants collected 3 miles north of Charlottesville, Va., and studied at the Blandy Experimental Farm of the University of Virginia. | $n = 36$ |
| <i>Rogers</i> | Seeds collected at Rogers, Benton Co., Ark., by the Soil Conservation Service. | $n = 18$ |
| <i>Rosebud</i> | Plants collected along roadside 13 miles n.w. of Rosebud, Gasconade Co., Mo., by Leslie Hubricht. | $n = 18$ |



Map 1. Distribution of *Tripsacum dactyloides* (exclusive of var. *occidentale*): small black dots indicate herbarium records; large black dots, $2n = 72$; open circles, $2n = 36$. This map summarizes the previously published information, the counts reported below, and unpublished information kindly supplied by Drs. L. R. Randolph and A. E. Longley, of the U. S. Dept. Agr.

Developing inflorescences were pickled in one part glacial acetic acid and two parts absolute alcohol, and the young anthers were smeared in Belling's acetocarmine the next day or as soon as convenient, following McClintock's directions as to ultra-clean slides and the gentle use of heat to spread the cells. *Tripsacum* gives the appearance of going through the reduction division at a later stage in the ontogeny of the inflorescence than does maize. Secondary inflorescences pickled just after the terminal florets were clearly visible above the enclosing sheaths were found in every instance to contain pollen mother cells in all stages from early prophase to metaphase. At metaphase the PMC is so elongated that nearly all the cells lie on their sides when smeared; polar views in which the chromosomes can be counted are seldom met with. It was found more practicable to make chromosome counts in diakinesis when the chromosome pairs are showing maximum repulsion. By studying this stage it was also possible to find cells in which an approximate notion of chiasma frequencies and positions could be obtained.

Results.—Chromosome numbers have been enumerated above, with the information as to where the plants were collected. Camera-lucida drawings are shown in fig. 1. In Map 1, the distribution of these plants is shown graphically along with that of those studied by Longley³, by Mangelsdorf and Reeves⁴, and with information graciously furnished by Dr. L. R. Randolph. Taken with the morphological data reported by Cutler and Anderson, Map 1 suggests that the varieties along the eastern seaboard are amphiploid ($n = 36$) and that there is a fairly widespread race ($n = 18$) of lower ploidy along the eastern edge of the Great Plains and in the adjacent prairies. Nothing is known cytologically about the peculiar *Tripsacums* reported from central Illinois,⁵ and the situation in Texas seems to be complex with counts of both $2n = 72$ and $2n = 36$ in the eastern part of the state. More field work in this area would be desirable but the changes wrought in the east Texas landscape by a century of intensive cultivation are so considerable that it might be very difficult, or even impossible, to determine the original relationships of these entities.

As in the related genus *Zea*, the chromosomes of *Tripsacum* undergo extreme contraction between pachytene and metaphase. Chiasma frequencies cannot be accurately determined, particularly at the later stages. At diakinesis it is often possible to make out chiasma frequency with a fair degree of objectivity, for some of the bivalents in a cell. Only very rarely are there cells in which the total frequency can be obtained. Figure 1 (above) shows a camera-lucida drawing of such a cell. The numbers given are minima; the actual total frequency might possibly be somewhat higher; it could not conceivably be any less. It gives an average frequency of just a little over two chiasmata per bivalent.

³ Longley, Albert E. Chromosomes in maize and maize relatives. Jour. Agr. Res. 28:673-687. 1924.

⁴ *loc. cit.*

⁵ Cutler and Anderson, *loc. cit.*

In the 18-paired *Tripsacum*s no multivalent associations were recognized and there were no irregularities at metaphase. Frequently one or two bivalents would still be dividing after all the others had divided and moved to the poles, as previously described by Reeves and Mangelsdorf. When carefully examined such cells were always found to be perfectly regular in every other way and the tardy bivalents were symmetrical and were normally aligned upon the plate. It seems likely that they represent some of the larger and longer chromosomes, since it is



Fig. 1. Camera-lucida drawings (all to same scale) of aceto-carmin smears of *Tripsacum dactyloides* pollen mother cells at diakinesis. Nucleoli represented by light stippled outlines. All show 18 bivalents except the lower left, which has 7 quadrivalents and 28 bivalents. Upper right, plant from Rosebud, Mo.; upper left, PMC from same smear drawn at a slightly earlier stage when the chiasmata are more clearly evident. (Numbers refer to estimated numbers of chiasmata for each bivalent; configurations which would have overlapped on the drawing are drawn out separately at the left); center right, plant from Fourche a du Clos, Mo., drawn at two levels with nucleolus repeated as a reference point; center left, plant from Dederick, Mo.; lower right, plant from seed collected at Rogers, Ark.; lower left, plant from Spencer Co., Ind.

quite evident that there is a good deal of variation in size between bivalents.

In the plants with a $2n$ number of 72, multivalent configurations were found in every cell. Both in the material from Virginia and that from southern Indiana, cells with 30 configurations were very common. Unfortunately, the size range of bivalents is so great and the contraction can be so extreme that it is not always possible to distinguish between a small bivalent and a large univalent. Nothing was seen which, by comparison with the diploids, was certainly a univalent although there was an occasional configuration which might possibly have been one. In those multivalents whose structure could be made out with certainty only quadrivalents were recognized. These were all open rings of 4 or open chains of 4. Closed figures of 8, closed rings of 4 (all 4 united at each end) cross-shaped quadrivalents, and rings of 2 united to chains of 2 were not seen, though in such highly contracted chromosomes some of these configurations would have been difficult to make out if they had actually been present. Disjunction of the multivalents seemed to be regular at metaphase, and no micronuclei or other irregularities were noted in young microspores.

Discussion.—Eighteen is the lowest number of chromosome pairs yet reported for any *Tripsacum* (Reeves and Mangelsdorf⁶; Longley⁷), but in the closely related genus *Manisuris* there is one species with 9 pairs of chromosomes⁸. This suggests that *Tripsacums* with 18 pairs of chromosomes may themselves be tetraploid. Since polyploidy of a high order is very frequent in the Gramineae this does not appear at all unlikely. Furthermore, the complex morphological relationships between *Manisuris*, *Rottboellia*, *Tripsacum*, etc., suggest that they may all be part of an intricate polyploid complex. *Manisuris cylindrica*, for instance, was originally regarded as a species of *Tripsacum*, to which genus it shows a very strong natural resemblance. However, it has perfect flowers, a character which technically would remove it completely from the tribe Maydeae. By various experts it has been assigned to the genus *Rottboellia*, to *Coelorachis*, and to *Manisuris*, nor is it the only species in this group of genera whose position has been generally uncertain. The fact that *Manisuris cylindrica* is almost identical with *Tripsacum*, aside from its perfect flowers and that it has half the chromosome number of the lowest reported *Tripsacum*, would suggest that the 18-paired *Tripsacums* are themselves tetraploid. However, since they show little or no multivalent association, they are most probably amphidiploid derivatives of distantly related diploids. The cytological evidence would suggest that the 18-paired *Tripsacums* might have a cytological formula of $XXYY$ where X and Y stand for sets of 9 chromosomes, and that *Manisuris* might be XX on the same notation. The taxonomic confusion in this group of genera is exactly what would have resulted had such inter-generic (and probably inter-tribal) reticulate relationships become established.

⁶ Reeves, R. G., and P. C. Mangelsdorf. Chromosome numbers in relatives of *Zea Mays* L. *Am. Nat.* 69:633-635. 1936.

⁷ *loc. cit.*

The chiasma frequencies and multivalent frequencies noted above can be used to suggest the possible relationships between the 18- and 36-paired *Tripsacums*. With a frequency of approximately 2 per bivalent (such as that reported above) and on the simplest possible assumptions we would expect an auto-tetraploid to form quadrivalents two-thirds of the time and pairs of bivalents one-third. (With 2 chiasmata per bivalent we expect one at each end. If among the homologous chromosomes 1, 2, 3, and 4, chromosome No. 1 pairs with No. 2, then at its other end it is equally likely that it pair with 2, 3, or 4. Pairing with 3 or 4 will produce quadrivalents, with 2 will produce 2 bivalents.) If the 36 *Tripsacums* are auto-polyploids we would expect two-thirds of them to produce quadrivalents and one-third bivalents. This would result in 12 quadrivalents and 12 bivalents, a total of 24 configurations per cell. If, however, they are amphipolyploids between related tetraploids (some such relationship as that between XXYY and XXZZ) then we would expect 30 configurations, the number actually observed. (Using XXYY and XXZZ to diagram the putative parental *Tripsacums* then we would expect the 9 sets of X's to form 6 quadrivalents and 6 bivalents, the Y's to form 9 bivalents and the Z's to form 9 bivalents, a total of 30 configurations).

The above computations should not be taken too seriously since they probably represent an over-simplification of what occurs and since the chiasma frequencies are based on estimates. However, they are put forward with more confidence since the observations preceded the computations. The estimate of 30 configurations was made so repeatedly in different smears of the 36-chromosomed plants from Indiana that a search was made through the records to find what has been noted about the Virginia plant when it was studied two years before. When the notes showed that it too had an overwhelming number of counts of 30, the computations were undertaken to see on what conditions such a number could be obtained. Since the Virginia and Indiana plants show certain constant morphological differences from the 18-paired plants of the prairies and Great Plains the simplest hypothesis was to assume that if the 18's were tetraploids of the constitution XXYY then the 36's were octoploids of the constitution XXYYXXZZ. The fact that the computations agreed exactly with the observations is more likely a happy coincidence than it is an exact scientific verification. It does, however, seem fairly certain that the 36's are not autopolyploids and that they must have roughly some such formula as the one suggested.

SUMMARY

1. The difficulties of maintaining a collection of *Tripsacum* plants are described.
2. Chromosome counts are reported for *Tripsacum dactyloides* collected at various points throughout its range. In the prairies and Great Plains this species has 18 pairs of chromosomes. Along the eastern seaboard it has 36 and in Texas both numbers have been reported.

3. The 18-paired plants undergo regular meiosis with no multivalent associations. Those with 72 chromosomes averaged 6 quadrivalents and 24 bivalents. Chiasma frequency in the former is at least 2 per bivalent.

4. On the basis of these observations and the general morphology of *T. dactyloides*, it is suggested that the 18-paired varieties of *Tripsacum* may be amphidiploids of the formula XXYY and that the 36-paired varieties arose as octoploids (XXYYXXZZ) between XXYY and XXZZ varieties.

HOMOLOGIES OF THE EAR AND TASSEL IN *ZEA MAYS*

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The exact correspondence between the variation of the male and female inflorescence of *Zea Mays* is a problem which has attracted a number of minds and has produced several theories, none of which completely satisfied the existing data. The morphological facts have been assembled by Weatherwax ('23, '35), and he, Collins ('19) and Kempton ('19) have reviewed the pertinent literature. After surveying all the existing evidence Collins' final conclusion was that, though he had used the hypothesis of a shortened and twisted central spike to explain the results in crosses between *Zea* and *Euchlaena*, "facts of other kinds are more easily interpreted by the theories of fasciation and reduction of branches . . . There are also facts that do not seem to accord with any of the theories yet proposed. Until the apparently contradictory evidence can be reconciled, it seems best to keep the several possibilities in mind and await additional evidence before attempting a complete interpretation." Though the facts reported below shed further light on the problem, Collins' words of caution are still in order and the complete solution, while perhaps not far distant, is still to be awaited. Though he disagreed rather completely with Collins on other points, Weatherwax's final conclusions ('23) concerning the ear were very similar. "The last word has not yet been said on the evolution of the ear of corn, and it cannot be said until further researches have corrected, amplified, and evaluated the data now at hand, and woven the results into a harmonious theory." [loc. cit. pp. 112-113].

Earlier workers were interested in the problem of ear and tassel relationships chiefly from theoretical considerations. With the development of large-scale scientific maize breeding in the U. S. cornbelt, it is now a problem of considerable economic importance as well. If a corn breeder could size up the potentialities of the ear, merely by examining the tassel, he could take many short cuts, both in the creation of new inbred lines and in maintaining their desirable characters.

Methods.—The general method of work is discussed in some detail since in the author's opinion it is of even greater significance than the results themselves (though, as will be demonstrated below, useful correlations have already been established by these methods). In beginning the work, a few tassels were examined in great detail, with particular reference to the structures considered significant by systematists: glumes, spikelets, pedicels, secondary and tertiary branches, etc. With these facts thoroughly in mind, as many kinds of maize as possible were grown and examined. A particular effort was made to secure rare and unusual varieties, especially those from Central America and South America.

The work was begun in 1941. By 1944 the general pattern of variation in tassel morphology was apparent. Then, for the first time, a serious effort was made to compare tassel and ear morphology in segregating families and in inbred lines of maize. A preliminary study of various inbreds from the U. S. Department of Agriculture and several agricultural experiment stations had indicated that this might be a fruitful method of investigation. Among the old well-established inbred lines used in modern hybrid corn breeding, there are many with extreme tassel types and ear types. Furthermore, they are practically pure breeding and they can be compared when planted in different soils, at different times of year and in different places. Through the kindness of the Pioneer Hi-Bred Corn Company, the inbred plots and breeding records of this company were put at my disposal in the summer of 1944. By a fortunate circumstance their breeding farm is not far distant from the Iowa Agricultural Experiment Station at Ames, where a further set of highly significant inbreds and hybrids was obtained from Professors E. W. Lindstrom and J. C. Eldredge. I am very much indebted to these individuals and institutions who have allowed me to study tassel morphology in their own experiments, most particularly to Mr. Raymond Baker of the Pioneer Hi-Bred Corn Company. His encouragement and cooperation have made possible this preliminary report though he is in no way responsible for its shortcomings.

The general method of work was to select either F_2 segregates or a series of inbreds with some outstanding characteristic of the tassel and then to examine the ears for possible correlations. When one was suspected, more material was examined to see if the correlation still held. The customary procedure in such cases was to walk rapidly through the breeding plots, keeping an eye out for tassels which were very extreme for the character under observation, and then to study the ears on these plants. When an ear-tassel correlation was at length apprehended, various methods of recording it were tried out. It was then measured precisely in a series of inbred lines, and the figures so obtained were compared not only with the actual ears borne by these inbreds but also with their progeny in controlled crosses. For instance, it was suspected that the length of the upper tassel branches was an important factor in ear length; Lindstrom's LA inbred line of maize was found to be an outstanding inbred line in the length of its upper tassel branches. Not only did it prove to have a long ear for an inbred; a reference to breeding records showed that on the average it had transmitted longer ears to its progeny than any of the other inbreds with which it was being compared. To summarize: tassel variation was studied in a general way for three years before precise correlations of ear and tassel were attempted. Even then, they were first run to earth by quick qualitative methods before they were submitted to statistical treatment.

It is unfortunate that much of the so-called quantitative investigation in this country is done in exactly the opposite fashion. In many laboratories measurements are taken by the hundred and are then submitted to mathematical analysis

in the hopes that useful results will emerge. This is putting the cart before the horse. It is a fundamental principle, too often ignored, that before a biological phenomenon is to be investigated on the mathematical level it must first be thoroughly analyzed on the biological level. One must first understand in at least a general sort of way what is happening in the material under investigation before he can set up an efficient measure of that particular phenomenon. The ear-tassel correlation problem is an instructive example. In terms of what one human being can accomplish in a life time, the numbers of features of maize ears and tassels which might be measured are almost infinite. It is scarcely to be wondered, therefore, that few significant results were obtained by those who studied ear-tassel correlation with an electric computing machine (Collins, '16; Kempton, '26). Statistical analysis has a useful place in biology but it must be preceded by biological analysis.

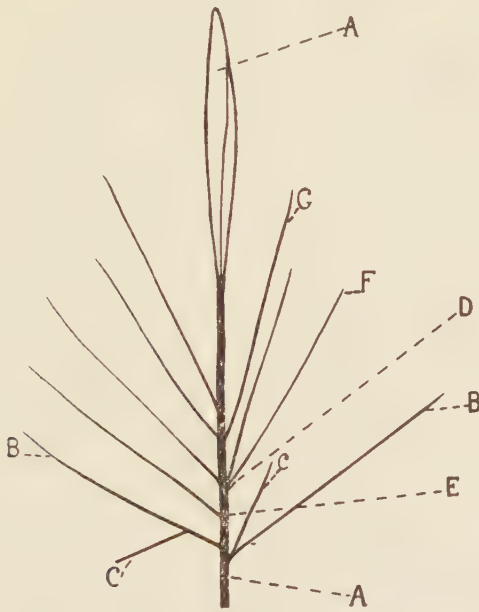


Fig. 1. Diagram showing main features of male inflorescence ("tassel") of *Zea Mays*. Further explanation in text.

Tassel Morphology in Zea Mays.—In order to grasp the following discussion it will be necessary to have the fundamental ground-plan of the male inflorescence of maize (the tassel in common speech) thoroughly in mind. Its branching system is illustrated diagrammatically in fig. 1; certain variations in the arrangements of the spikelets are shown in fig. 2. The tassel always consists of a primary axis (AA), fig. 1, usually with a certain number of secondary branches (B, F, G, etc.). The lower secondaries may themselves branch at the base giving rise to



Fig. 2. Diagram showing variation in spikelet arrangement on secondary tassel branches in North American strains of *Zea Mays*. 'A' shows very slight condensation of internodes; 'B' shows higher condensation; 'C', the extreme of a common North American tendency, the shortening of the pedicel in the pedicellate spikelet. Further explanation in text.

tertiary branches (C). The primary axis is terminated by the central spike (A). The secondaries may all arise separately from the primary axis or a part of them may be whorled (D) or, in rare cases, they may all be in whorls of 2 or 3. The number of secondaries varies widely even under the same cultural conditions and is usually quite constant in inbred lines. There are occasionally only 1 or 2 (in rare cases none), or there may be up to 40 or more in each tassel. The length of the secondaries varies greatly as well as their comparative lengths along the tassel.

Figure 2 diagrams the manner in which the spikelets are arranged upon the branches of the inflorescence. The maize of the American corn belt is highly

variable for this character, as will be discussed below. 'A', in fig. 2, diagrams the simplest arrangement and one which is, from a technical agrostological point of view, the normal one for *Zea Mays*. The spikelets are arranged in pairs, one spikelet in each pair being sessile and one pedicellate. In North American maize there is great variation in the length of the pedicel and in some inbred lines the condition may be like that illustrated at 'C' where the spikelets are in pairs but the members of each pair are practically indistinguishable in pedicel length.

All North American dent corn has a considerable number of condensed or telescoped internodes as illustrated in 'B'. Sometimes the condition is no more extreme than illustrated at 'A'. The fifth node from the apex is really two nodes and bears two pairs of spikelets instead of one. The example shown at 'B' is by no means extreme, and there are many inbred lines and Mexican varieties which show twice as much condensation as this. The tassel branch segment in 'B' has exactly as many spikelet pairs as 'A' and 'C' but many of the internodes are condensed. From the apex to the base the number of spikelet pairs at each apparently single node are 3, 3, 1, 2, 2, and 1. Technically, of course, there are 3 fused nodes at the first, each with its own pairs of spikelets, 3 at the second, and so on down the stalk.

Inbred lines of maize vary in the angle at which the secondaries leave the primary axis and the angle is usually surprisingly constant for each inbred line. In certain inbreds it is sometimes constantly under 10 degrees; in other inbreds it may even exceed a right angle.

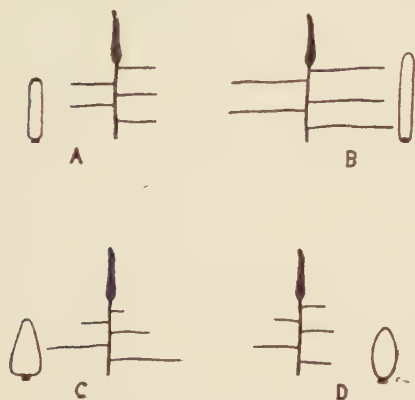


Fig. 3. Relation between tassel shape and ear shape in *Zea Mays*; highly diagrammatic. Further explanation in text.

Maize from different parts of the New World, as well as inbred lines, varies greatly in the position at which the lowest spikelet pair is set on the secondary. In some Mexican varieties and certain commercial inbreds it is so close to the base of the secondary that it almost seems to arise from the primary axis. In most high-altitude South American varieties, the secondary has a long basal internode below the first spikelet pair. In our notes, this is referred to as the "sterile zone" and is usually measured on the third secondary from the base of the tassel.

Correlations.—It may make the discussion easier if we anticipate the general conclusions from the data before presenting the results in detail. The correlations between tassel and ear are those which would result if the ear were composed of branches fused spirally about a central cylinder (see fig. 3). The actual correlations are a fact. Their interpretation is quite another matter and is discussed

briefly on page 338. Figure 3 demonstrates, for several extreme tassel types, the fairly precise correspondence between the "profile" of the tassel branches and the shape and size of the ear. However, all of these patterns are affected by the degree of condensation which varies independently of the number of tassel branches and their absolute and relative lengths. It will, therefore, be necessary, first of all, to discuss ear-tassel correlations for condensed internodes.

Condensation.—As has previously been explained, the internodes of North American maize tassels may frequently be condensed or telescoped. Sometimes an internode is extremely shortened but is still visible as a separate internode. More frequently 2, 3 or even 4 internodes are so foreshortened that they give the appearance of a single node bearing 2, 3, or 4 pairs of spikelets. It is, in other words, a kind of controlled fasciation which operates throughout the plant. In the ear, it is one of the factors controlling row number. As will be demonstrated below, there is in North American maize a surprisingly close correlation between the condensation of the tassel and the degree to which row number is increased above 8 or 10 rows. For several reasons, condensation can be studied much more effectively in the tassel. In the first place, the tassel is apparently much more sensitive, and a low degree of condensation which will not reach a threshold of expression as to row number can be exactly measured there. In the second place, the ear is a highly complex organ in which it is difficult to detect the individual effects of various developmental factors. The tassel is much more simple and in it the effects of condensation can be studied independently of other factors. In the tassel, for instance, one may study condensation, the development of secondary and tertiary branches, and whorled branches vs. alternate or spiral branching, and all three can be followed as independent variables. In the ear they all affect row number in one way or another.

The genetic background of condensation is obscure. It seems to be a kind of fasciation due either to a single mutant gene and a large number of minus modifiers or to a large number of genes which produce the same general effect. It has a pronounced geographical distribution which is exactly that of denting. Though dented kernels and condensation are different things genetically they are both found in an exaggerated degree in the Mexico City-Toluca neighborhood (Anderson, unpublished) and seem to radiate from there in all directions. From archeological evidence we know they have been there for at least a thousand years and that it is apparently the center to which all our North American dent corns can be traced back.

The number of spikelet pairs per internode (and therefore the degree of condensation) varies within very wide limits, and these extreme types are characteristic of two widely separated areas in the New World. The varieties of high altitudes in South America have little or no condensation in the secondaries. A specimen tassel grown in the United States from Peruvian seed had the following number of spikelet pairs per node on its lowest secondary branch (scored from

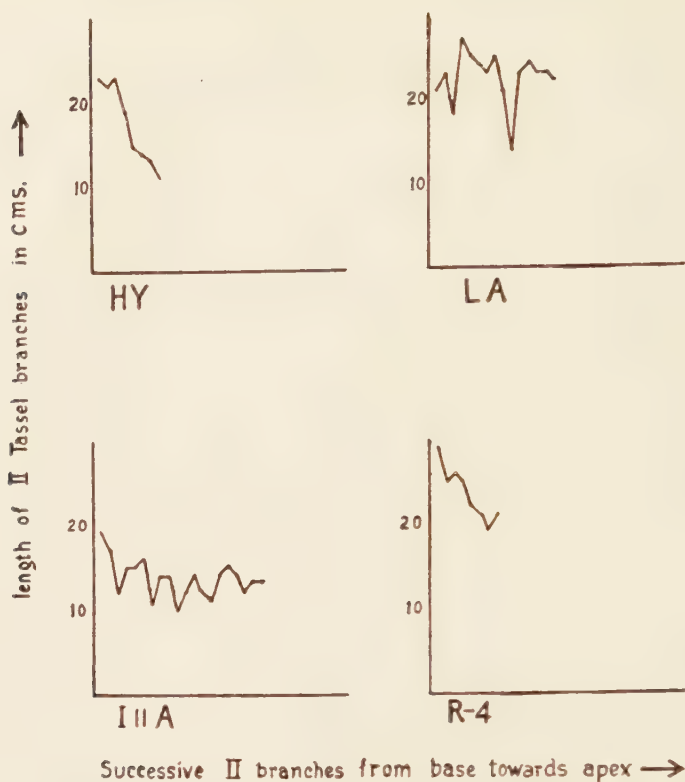


Fig. 4. Tassel branch profiles of four inbred strains of *Zea Mays*. The lengths of successive secondary branches are plotted, one after the other, and joined by a line. Further explanation in text.

much of the corn of the U. S. corn belt, the ear row number is equal to roughly ten times the condensation index, or in mathematical notation:

$$\text{Row number} = 10 \text{ CI.}$$

As has been suggested above, row number and row pattern are affected by various factors but in much of the maize of the United States, condensation is the chief variable. For all practical purposes we can assume that North American maize has a "fundamental" row number of 8 or 10 and that any increase above this number will be directly proportional to the Condensation Index as calculated from the tassel. This is not just a theory; it has been experimentally verified in a wide variety of inbred, hybrid, and open-pollinated material. Before discussing it, it will be necessary to review the evidence for variability in row number. This character, as might be expected, is influenced not only by inherent capacity for many or few rows, but by the vigor of the plant and by environmental influences. Even highly homozygous inbreds and first-generation hybrids may vary considerably in row number. The latter, as is well known, is always an even number since the fundamental variable is the number of alicoles, each one of which gives

rise to two rows (Collins, '16). A hybrid which is characterized by 14 rows may bear a good many ears with 12 and with 16 rows. A weak inbred which averages only 14 ears may behave in crosses as though it averaged 16, etc.

One of the most precise tests for the exact correspondence between row number and the Condensation Index was afforded by Lindstrom's PR inbred and its remarkable mutant PR-M. As Lindstrom has stated ('40), the former is potentially 20-rowed and the mutant is potentially 16-rowed. Fifteen tassels of each were examined. The average Condensation Index for the PR tassels was 2.2; for the PR-M tassels 1.7. If we assume that the row number divided by the Condensation Index will give us what the rowing would have been without condensation, we may divide 20 by 2.2 for PR and 16 by 1.7 for PR-M. The answer to the nearest round number is 10 for each. In other words, the higher degree of condensation in the tassel of PR as compared to PR-M is exactly proportional to the increase in ear row number.

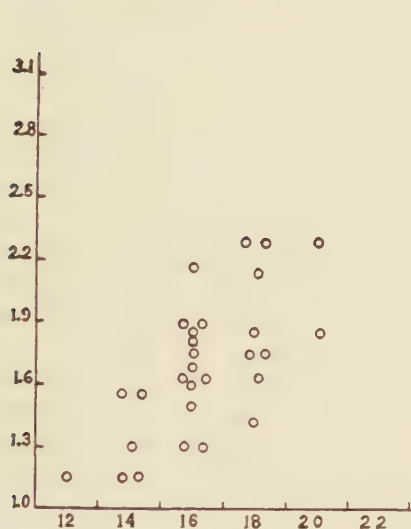


Fig. 5. Scatter diagram showing the correlation between tassel-node condensation and ear row number in a group of F_1 crosses between inbred lines of commercial corn. Vertical scale, average condensation index of the two parental inbred tassels. Horizontal scale, number of rows of kernels on the ears of the F_1 hybrid plants.

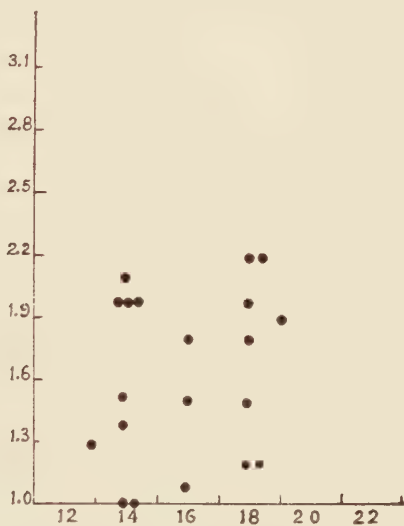


Fig. 6. Scatter diagram showing correlation between tassel-node condensation and ear row number among 21 plants of a back-cross between two inbred lines of yellow dent corn. Each dot represents a single plant. Vertical scale, condensation index of the tassel; horizontal scale, number of rows of kernels on the ear.

Another precise test was afforded by a series of standard commercial inbred lines of maize and their F_1 hybrids, selected from breeding plots of the Pioneer Hi-Bred Corn Company. The inbreds were being grown in short rows for observation. After a quick inspection, a single representative tassel was chosen from each inbred, and the Condensation Index was calculated in the manner described above. The average Condensation Index for any two inbreds was then calculated

and compared with the actual row number obtained in a hybrid between these two inbred lines. Here again, only one plant was examined. No conscious selection was made other than to see that the ear was obtained from a healthy plant with no obvious malformations. The correlation between tassel condensation and ear row number is presented in fig. 5. Considering the variability of row number this is a remarkably high correlation, especially when one considers that neither tassel condensation nor ear row number was an average value, but was merely a single selected individual. It will be noted that for lower values of the Condensation Index the row numbers are on the average about 10 times the Index but that for higher values these potentialities are not realized. It may be that, under the conditions of the experiment (the plants were being grown three to a hill), the plants with high condensation were not able to reach their full potentialities. It is also possible that in corn-belt maize there has been a strong selection of modifying factors which would keep the high degrees of condensation under control. It is certainly true in Japanese Hull-less popcorn, where these "bearpaw" ears have not been selected against, that highly condensed tassels are accompanied by equally highly condensed ears. One tassel selected because it was highly condensed along its whole length, with an average condensation of 3.3, had 32 rows of kernels; a much less condensed tassel, with an Index of Condensation of 2.1, had 24 rows of kernels.

Figure 6 shows the same kind of scatter diagram in a population where the effects of environment are much more severe and a less close correlation would be expected. A hybrid between two inbred lines was back-crossed to one of the parents, and these were planted three to a hill in a large plot. In the previous example, while the hybrids were subject to this same crowding, they were all planted with individuals of their own genetic constitution, and interaction between plants was relatively constant throughout the experiment. In this back-cross the plants varied in their general vigor. A strong plant which happened to be in the same hill with two quite weak siblings had an excellent opportunity to reach its full potentialities; a weak plant in the same hill with two very strong ones could not have been expected to do so.

Finally, fig. 7 diagrams a larger population in which the interaction between the three plants in each hill is somewhat less extreme. In this case ear-to-row tests were being made of an open-pollinated strain of a long-eared yellow dent. One healthy, vigorous plant was selected in each row and its row number and Condensation Index were obtained.

There is even a correspondence between the condensation *pattern* of the basal-most secondary branch of the tassel and the flattening of the ear. If the tassel branch is highly condensed along its entire length, then the ear will be a true "bearpaw." If the tassel branch is highly condensed at the tip but much less so below, then the ear will be more or less circular in cross-section with a flaring, usually two-pointed apex. If the tassel branch is highly condensed at the base but runs out into a long uncondensed portion, then the ear will be broadly

Tassel profile and ear shape.—As shown schematically in fig. 3, there is a surprisingly close correspondence between tassel branch length and ear length and between the relative lengths of successive tassel branches and the shape of the ear. If the tassel branches are all long, as in fig. 3, 'B', then the ear is long and cylindrical; if they are all short (fig. 3, 'A'), then the ear is short but still cylindrical. If the branches get successively shorter towards the apex, then the ear tapers sharply and regularly (fig. 3, 'C'). If they are short both at the base and the apex and longest in between (fig. 3, 'D'), then the ears have a kind of "hand grenade" shape as in certain sorts from South America.

This correlation is more than a general one between different races of maize; if used in conjunction with the other correlations reported in this paper it may even be used to judge between related inbreds. It apparently is highly correlated not only with the actual shape of the inbred ear but also with the behavior of the inbred in crosses. Tassel branch diagrams are presented in fig. 4, using a modification of the simple method recently described by Anderson and Schregardus ('44). It will be seen that the "profile" of the tassel established in fig. 4 is an excellent reflection of the known behavior of these inbreds. Inbred LA is known to produce long cylindrical ears in single crosses with other inbreds while inbred HY is also notorious as producing sharply tapering ears in crosses with other inbreds. Preliminary indications are that the tassel profile may even be a better indication of ear-shape potency than the actual ear of the inbred itself. Some 40 inbreds were carefully examined and their tassel profiles were compared with the ears. All agreed in a general sort of way though there were a few exceptions. These exceptional profiles agreed better with the breeding records than the ears themselves. Figure 4 shows a case in point, the profiles of inbreds Ill. A and R-4. The profile of the former suggests a short, nearly cylindrical ear. The profile of R-4 suggests a long ear, tapering pretty sharply, though not as extreme as HY. The actual ears of these inbreds are somewhat as indicated, but when compared with each other they are very much alike; much more so than the tassel profiles. However, both of these inbreds are widely used commercially. It is well known that in hybrids, R-4 produces a much longer but more tapered ear than does Ill. A.

In the material which has been investigated there is even some indication that if the first one or two tassel branches are markedly longer than the rest there will be a tendency for the basal portion of the ear to be somewhat larger. This correlation rests on scattered observations and needs to be carefully tested with lines which are reasonably constant for other characters but differ in the basal enlargement of the ear or the length of the lowest one or two tassel branches.

Tertiary tassel branches and irregular rowing.—The kernels of an ear of maize may be spaced either evenly or unevenly. A little examination will show that the unevenness is due to two quite different factors. The rows may be regular but the kernels set crookedly in the row, or the rows themselves may be irregular

in spite of the fact that the kernels are set straight in the rows. This latter condition is, among other things, correlated with the number of tertiary branches on the lower secondary branches of the tassel. Here again, the two extreme conditions have marked geographical distributions. The common dent varieties of the American corn belt have an intermediate condition between these two extremes, and ordinarily have 1 or 2 of the lower secondaries which bear tertiary branches, usually not more than 1 or 2 tertiaries arising from each. In the Peruvian area 6 or more of the basal secondaries may bear tertiaries. There are frequently 5 tertiaries on the basal-most secondary, and the larger tertiaries may themselves give rise to short branches of the fourth order. Similar tassels are also to be found in Guatemala. The other extreme is found most highly developed in Mexico where in spite of the fact that the tassels are often very large, tertiary branches are few or none.

If the ear were formed *as if* the tassels were wrapped spirally about a central core, then one might expect these short tertiary branches to upset the rowing. Such is probably the case. As with the factor for condensation, there is apparently a lower threshold for expression in the tassel than on the cob. A tassel with one or two tertiaries is not always accompanied by irregular rowing. However, inbred lines characterized by highly irregular rows have a high degree of tertiary branching in the tassel. There even seems to be a rough correspondence between the comparative length of the tertiaries and the place on the ear where the irregularities appear. These may take two forms. Ordinarily, they show as a place where the row runs out. Sometimes, however, they merely appear as an extra grain inserted between two adjacent rows.

Further correlations are suspected but will require detailed examination of critical material to establish. These are as follows: (1) a positive correlation between the size of the primary axis at the base and the size of the shank and cob, (2) a positive correlation between the number of tassel branches and the comparative size of the pith zone in the center of the cob, (3) a negative correlation between the angle made by the primary axis and the secondary branches of the tassel and the brittle-stiffness¹ of the main stalk of the corn plant, (4) a correlation between very large, rough, pointed spikelets and long, more-or-less pointed kernels.

Discussion.—The correlations outlined above are definite enough to be of some use in practical maize breeding. This does not necessarily mean that they are decisive evidence in the old controversy as to whether the ear of corn is homologous with the central spike of the tassel or whether it is homologous with an entire tassel of fused branches. When we come to understand the tassel and the ear not merely as end products but in terms of the actual forces which mould them as they are, we may find that both of these concepts have their place. It is quite possible that, in so far as some forces are concerned, an entire ear is like the central

¹ No one English word expresses this quality.

spike of the tassel, but that in terms of other forces it is more exactly homologous with tassel branches fused spirally side by side. An extension of the general method described in the introduction should make it possible to settle such questions fairly definitely.

The observations reported above do provide fairly clear evidence with regard to the old controversy as to whether or not the ear of maize is fasciated. The "condensation" reported above is a kind of regular, controlled fasciation which only occasionally becomes so extreme as to produce elliptical axes and multiple growing-points. The new evidence also suggests quite as clearly that fasciation is only one of several forces and that in North American maize it operates only in ears of more than 8 or 10 rows. The whole history of the maize ear is much too complex to discuss here even in a preliminary fashion. Understanding that the condensation of North American maize is a special feature and that it apparently traces back to the Mexico City-Toluca area and is tied up with the history of dents and "bearpaw" popcorns should enable us to approach the larger problem more intelligently. Apparently, primitive South American maize had a whorled tassel and a short, ovate or top-shaped ear with regularly disposed kernels but no straight rows, as we know them in modern maize. Some unexplained agent, perhaps *Tripsacum* (Mangelsdorf and Reeves, '39), introduced long straight rowing and alternate or spiral tassel branches. The extremely simple 8-rowed flints are not among the older prehistoric remains either in South America or in the American Southwest. The straight 8-rowed ear is apparently a highly derived rather than a primitive condition in *Zea Mays* (if we consider that remarkable aggregation of forms *as a whole* and not merely from the point of view of the American corn belt). Increase in row number in South American varieties is accompanied by an increase of condensation in the central spike but apparently not in the tassel branches. This is one of many points concerning condensation that needs further investigation.

Little has been said concerning the genetics of any of the characters described above. They are all apparently multiple-factorial. Preliminary evidence suggests that the factors are not scattered at random through the chromosomes. An extension of the methods of analysis outlined above should make it possible to begin the exact genetic study of quantitative characters in maize. Emerson and his co-workers have already assembled a series of marker genes and an effective cooperation between different laboratories. Unfortunately, however, the chief character (ear row number) which has so far been investigated (Emerson, '32) is one which does not lend itself well to exact analysis. Since the difference between an easily recorded character and an easily analyzed character does not seem to be generally understood it may be well to amplify this *dictum*.

Ear row number is a good example of a quantitative character which is easy to record exactly but difficult to analyze. Any ordinary ear of maize has just so many rows and there is no quibble about it. However, we are not interested as geneticists in the number of rows; we want to find out something about the

forces which go to make low row number or high row number. As has been demonstrated above, these forces are of various kinds, *each one a quantitative multiple factor character in itself*. Before we can analyze the genetics of row number we must, first of all, break it down into its component forces. The section on "Condensation" presents data which suggest that condensation is *one* of these components. With the method of tassel scoring outlined above, it should be possible to study the genetics of this primary multiple factor character and learn where the genes for condensation are and how many there are and how they interact. The other factors affecting row number will then be easier to analyze, but serious genetic analysis must again be preceded by morphological detective work.

Just as the early work on the genetics of eye-color mutants and wing mutants in *Drosophila* was based upon long hours of study and scrutiny by such gifted observers as the late Calvin Bridges, so any serious attempt to study the genetics of quantitative characters must be preceded by explorative observation. It is generally admitted that the genetics of quantitative characters is much more difficult than that of single factor mutations. After a decade of work, I am convinced that the preliminary observational analysis of quantitative characters presents unsuspected difficulties; difficulties, furthermore, of a higher order of complexity. It is indeed a research field in its own right. Although plant material is apparently easier to analyze morphologically than either vertebrate or insect material, it will require long and coöperative preliminary research if problems concerning quantitative characters are to be brought to the level where they are ready for genetic analysis. A series of apparently unrelated papers which have emanated from this laboratory in the past decade (Anderson and de Winton, '35; Anderson, '39; Anderson and Ownbey, '39; Anderson and Hubricht, '43; Anderson, '44; and Anderson and Schregardus, '44) are all connected in one way or another with this problem. While some of them have so little apparent connection with plant genetics that they could not have been published in a journal devoted to that subject, they are all concerned with multiple factor genetics. They represent various attempts to work out methods for analyzing quantitative characters on a morphological level. In this paper I have attempted to demonstrate how such techniques might be applied to practical maize-breeding problems.

SUMMARY

1. The methods used in this study are described. The necessity of analyzing the material on a biological level before statistical methods are applied is stressed and illustrated by examples.
2. Variation in the tassel (the male inflorescence of *Zea Mays*) is described, character by character, and methods of recording it exactly are outlined.
3. Evidence for the following ear-tassel correlations is presented:
 - a. Tassel internode condensation and increase in row number.
 - b. Tassel branch length and ear length.

- c. Tassel branch pattern and ear shape.
 - d. Tertiary branches and irregular rowing.
4. In North American corn, the relation between tassel condensation and row number is surprisingly exact. In general, it is close to the following equation:
- $$\text{Condensation Index} = \text{row number} / 10.$$
5. The geographical distribution of tassel condensation is discussed. It reaches its highest development in the Mexico City-Toluca area which is also the center for extreme denting.
6. The problem of homologies between tassel and ear is briefly discussed. It is tentatively concluded that in so far as the actual forces are concerned *both* the fused tassel branch hypothesis and the central spike hypothesis may be essentially true.
7. The application of these facts to the genetics of quantitative characters is discussed briefly. Using condensation as an example, a distinction is made between multiple factor characters which can be recorded exactly and those which can be analyzed exactly.

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EXPLANATION OF PLATE

PLATE 17

Three ears which illustrate the correspondence between the condensation of nodes in the tassel and the increase in row number of the ear: Left, inbred yellow dent Os 420; center, "bearpaw" dent from Mexico; right, open-pollinated yellow dent from Iowa. (N. B. This ear is right side up; the feature at the apex is the expanded tip of the cob.)

Condensation indices and condensation patterns for these ears are as follows, the figures representing the number of spikelet pairs per node beginning at the base of the lowermost tassel branch:

Inbred Os 420

C. I. = 1.4

1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 3, 1, 1, 2, 1, 1, 1, 1, 1, 2, 1, 1, 2, 1, 1, 1

"Bearpaw" dent

C. I. = 3.2

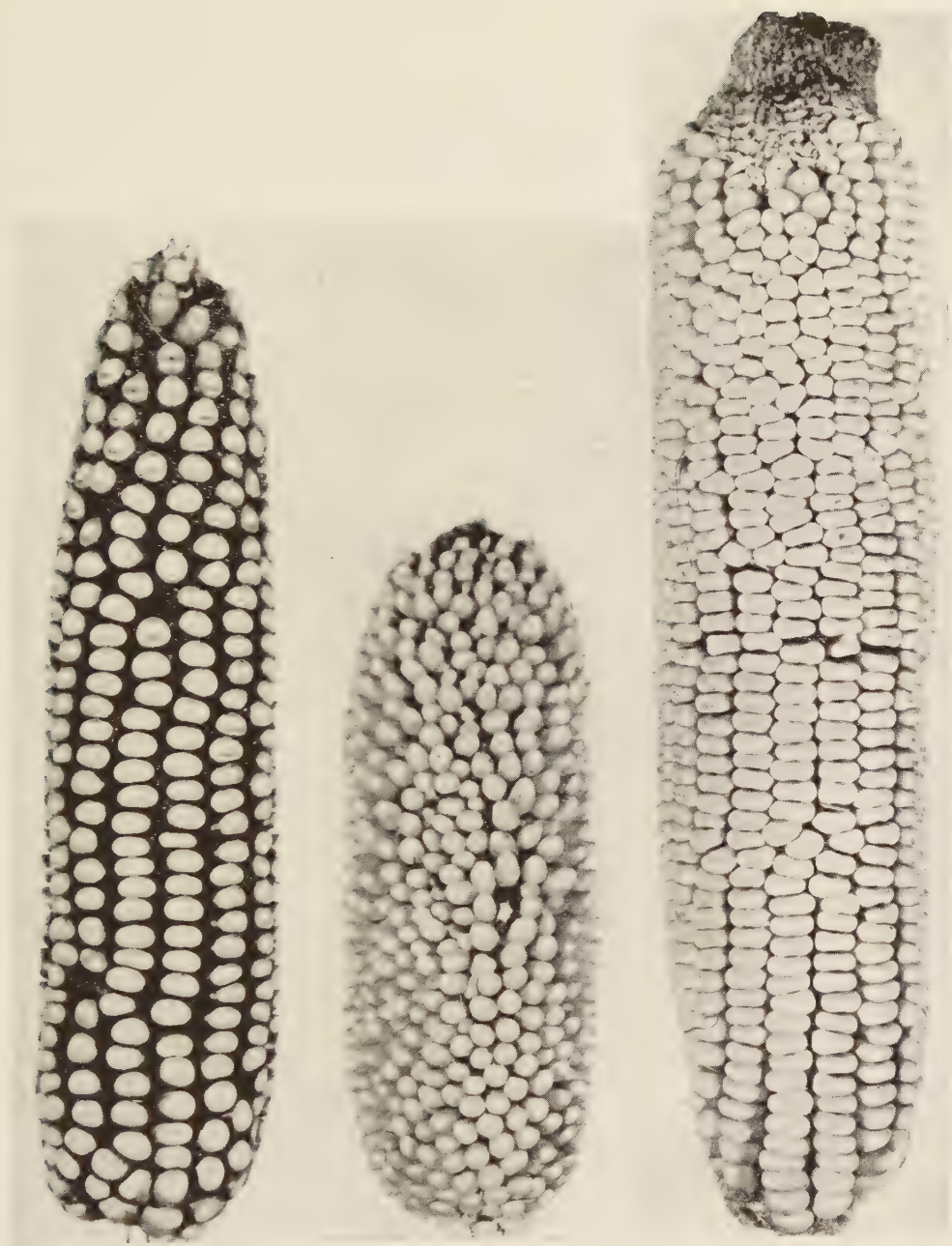
2, 3, 3, 2, 2, 2, 4, 4, 5, 3, 4, 3, 3, 3, 3, 4, 2, 4, 2, 3, 3, 3, 3, 2, 1, 3, 3, 3, 3, 5, 4, 3, 4, 4, 3, 3, 4, 2, 3, 3, 4, 2, 2, 4, 3, 4, 4, 3, 2, 3, 2, 4, 3, 2

Open-pollinated yellow dent

C. I. = 2.9

1, 1, 1, 1, 1, 2, 2, 2, 1, 2, 2, 2, 1, 3, 3, 1, 1, 2, 3, 3, 3, 4, 3, 5, 4, 5, 4, 5, 4, 5, 4, 5, 4, 4, 4, 1, 3, 1, 3, 2, 3, 1, 2, 2

Further explanation in the text.



ANDERSON—EAR-TASSEL HOMOLOGIES

TWO COLLECTIONS OF PREHISTORIC CORN TASSELS FROM SOUTHERN UTAH

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The extreme variability of *Zea Mays*, while discouraging to the novice, will make collections of prehistoric maize particularly significant when this variability is at length understood and catalogued. In this connection, it is unfortunate that more well-preserved male inflorescences (corn tassels in common speech) are not represented in archeological collections. While they do not present as many diagnostic features as the female inflorescence (the ear) they are by no means to be despised, particularly since their variation is comparatively easy to measure objectively and exactly. The following account has been prepared partly as a demonstration and partly because these particular collections present features of general interest. Both are from expeditions organized by the Peabody Museum of Harvard University. I am indebted to Dr. J. O. Brew for the opportunity of studying this interesting material and for much pertinent information.

The two collections are roughly contemporaneous and according to current archeological practice in the Southwest would be dated at about 1000 A.D.¹ (see caption fig. 3 for exact citations). One collection consisted of twelve more-or-less perfect tassels from Floating House Ruin on the Arizona-Utah border. The other came from a small cave at Alkali Ridge in southeastern Utah. As illustrated in plate 18, it consists of ten bunches of tassels neatly tied together with a strong withe, apparently of willow bark. The tassels are all just barely ripe; the anthers are developed and little or no pollen had yet been shed. All are neatly laid side by side, pointing the same way. All were either originally trimmed or have subsequently been broken. To a student of maize the most interesting feature of the collection is its comparative uniformity for technical characters, indicating a careful selection of seed stocks on the part of those who grew it. The plant-to-plant variation is no more than is found in such highly selected modern varieties of maize as Golden Bantam sweet corn or the white flour corn of the Hopi. It might be argued that the uniformity is merely a reflection of the innate lack of variability in a widespread primitive variety. On the contrary, such studies of plant-to-plant variation as have been made with Basket Maker maize² indicate that it was high.

After the collections had been photographed, the tassels were moistened to make them less brittle and the more-or-less complete tassels were then scored for

¹ Those unfamiliar with the archeology of the American Southwest will find useful summaries in: Roberts, Frank H. *Am. Anthropol.* n. s. **37**:1-35. 1935; and Bryan, Kirk. *Ann. Assoc. Am. Geog.* **31**:2; 9-226. 1941.

² Anderson, Edgar, and F. D. Blanchard. *Am. Jour. Bot.* **29**:832-835. 1942.

as many significant features as possible. While to the casual observer the male inflorescence of maize is so featureless as to be of no special interest, it is actually a complicated organ with a very definite ground-plan. The outstanding features are diagrammed in fig. 1, and a complete scoring of the tassel illustrated in plate 19 is presented in text-fig. 2. The maize tassel is built upon a primary axis terminated by the CENTRAL SPIKE (A, fig. 1), along which the spikelets are arranged in many rows (in some South American varieties they are in whorls of 3 or more). Below the central spike are the SECONDARY BRANCHES 'B', 'F', 'G' whose number varies greatly in different races of maize. The lowermost secondaries may bear TERTIARY BRANCHES 'C', and in some South American varieties these may even produce branches of the fourth order. The secondaries may arise

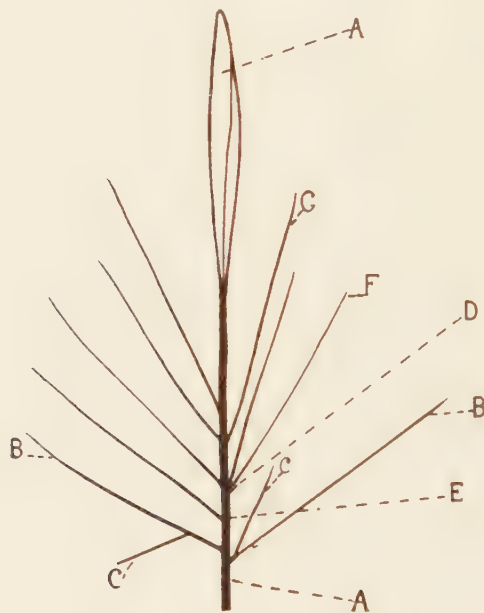
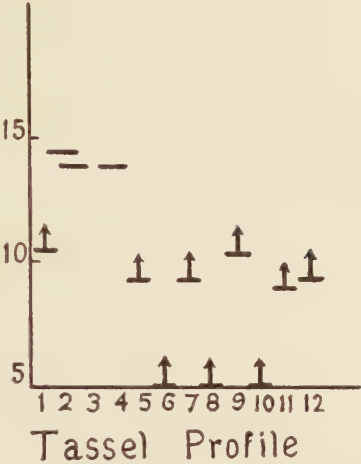


Fig. 1. Diagram showing main features of the male inflorescence (tassel) of *Zea Mays*, with particular reference to the usual type in North America. Further explanation in text.

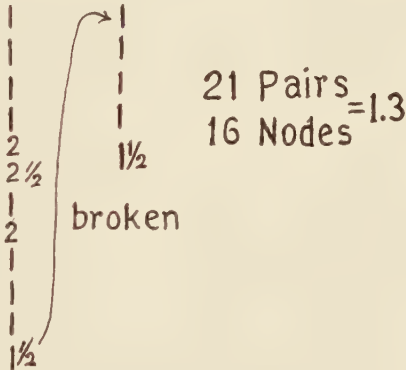
singly from the main axis or may be in WHORLS (D) of two or more. On the secondaries the SPIKELETS are arranged in pairs, though, as will be shown below, there are departures from this regular arrangement in North American maize. In each pair one spikelet is ordinarily pedicellate and one is sessile, but in North America the pedicellate spikelet may be so subsessile as to be indistinguishable from its neighbor. In South American maize the secondaries often have a long sterile zone at the base of the secondary branches which is without spikelets. In the Southwest and in Mexico this zone is short or is lacking altogether. The

length in c.m.
arrow indicates that the top was broken



Number of II branches 12
" " Nodes 8
Av. " II's per node-1.5

Number of spikelet pairs
at each node of lowermost
II branch, in order from
base to apex



III's on basal II ----1
III's on next II ----0
length of sterile zone--0
glume length in MM--12

Condensation Index

Fig. 2. Score sheet for the actual tassel illustrated in plate 19. Further explanation in text and in Anderson, Ann. Mo. Bot. Gard. 31:325-342. 1944.

length of the spikelets varies between different races of maize, and many of the southwestern varieties have *glumes* (the main feature of the spikelets) which are 12-15 mm. long.

As has recently been demonstrated³, all North American dent corns show a greater or lesser amount of *condensed* or telescoped internodes in their tassels, and this same condensation (a kind of controlled fasciation) is one of the factors responsible for the higher row number on the ears of these varieties. However this condition may have arisen, it is strongly centered geographically about the Mexico City-Toluca region. Condensed internodes in the tassel of a North

³ Anderson, Edgar. Ann. Mo. Bot. Gard. 31:325-342. 1944.

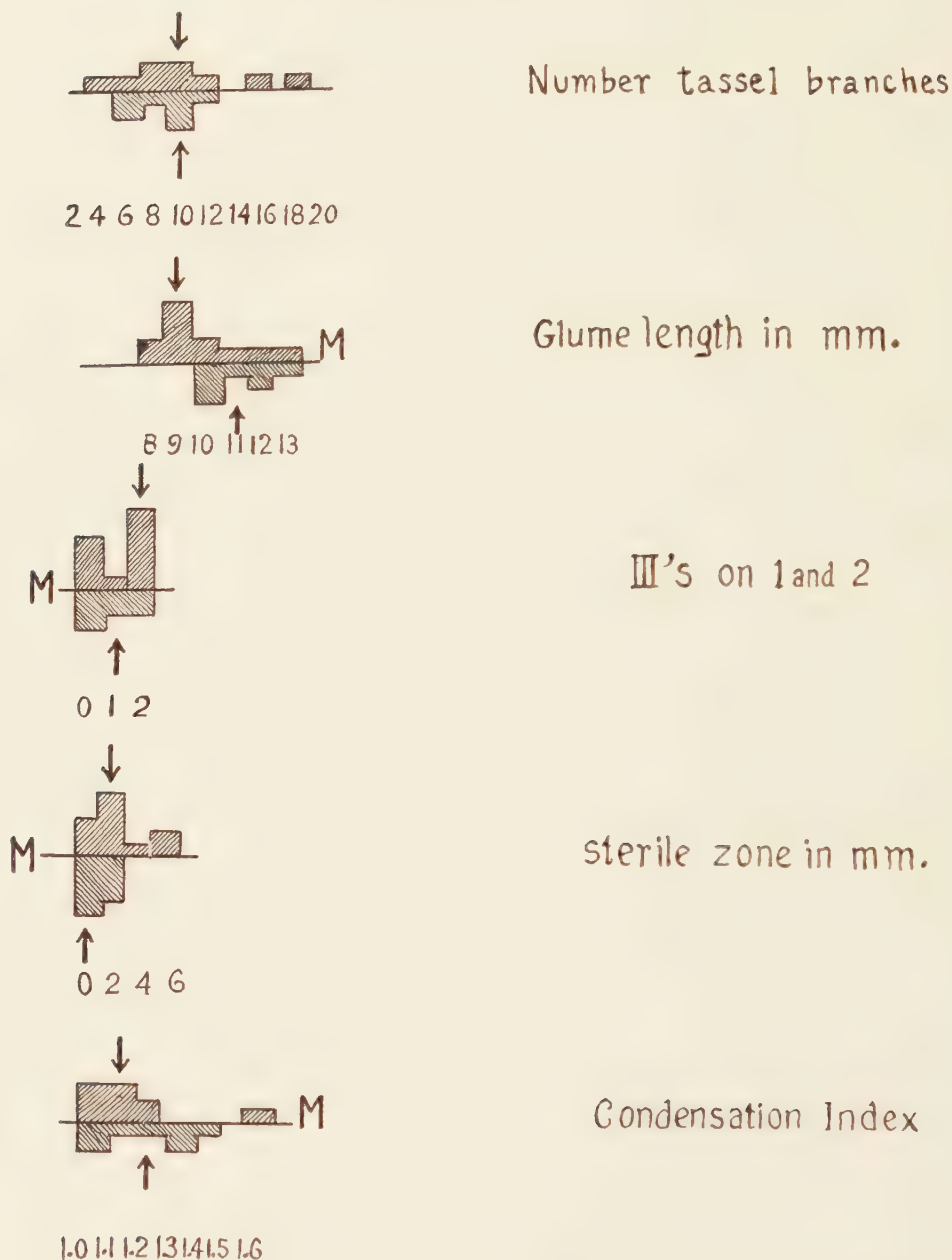


Fig. 3. Frequency distributions for five tassel characters for two prehistoric collections. The two are diagrammed from the same base line: upwards, frequencies for the collection from Floating House Ruin, Peabody Museum, No. 33-62-10/2118 (Room 2A above floor A); downwards, frequencies for the collection from Alkali Ridge, Peabody Museum, No. 33-44-10/3572 (small cave $\frac{1}{4}$ mi. from site Ab 7-13, Peabody Museum, Southeastern Utah Expedition). "M" represents the direction in which Mexico City tassels would score. Though the two frequencies are similar, the lower set (Alkali Ridge) is slightly more Mexican-like.

American variety of maize therefore imply a connection of some kind with the maize of that area, since high condensation seems to be too complex genetically to have arisen repeatedly. An exact method of scoring this condensation has recently been described³, and the Condensation Index derived from the tassel permits a fairly accurate estimate of the row number of the ear in North American varieties. The *Condensation Index* is calculated as shown in fig. 2. It is the average number of spikelet pairs per apparent node on the lowest secondary branch (see Anderson, *loc. cit.* for further details). After the Condensation Index the next most significant fact concerning the male inflorescence is the *tassel profile*. This is merely a diagram like the one illustrated in fig. 2. It shows the length of successive secondary branches in order from the base to the apex. In general, it is closely correlated with the size and shape of the ear³. In fig. 2, unbroken secondaries are indicated in the profile diagram by a bar, and broken secondaries by a bar with an arrow.

Frequency diagrams for the two collections are shown in fig. 3, the frequencies for *Floating House* being diagrammed upwards and those for *Alkali Ridge* downwards, from a common base line. The arrows indicate the averages (medians) for each of the five characters. There is no difference in the two averages for tassel branch number; for the other four characters there are slight differences. These are scarcely significant statistically, being based upon such small numbers, but biologically they may mean something since they are all in the same direction. For all four characters the Alkali Ridge collection differs from the Floating House series by being slightly more like the maize of the Mexico City-Toluca region. This well-marked geographical type (Mexican Pyramidal of Anderson and Cutler) has long glumes, few tertiaries, an extremely short sterile zone and a very high condensation index. Since the slight differences of the Alkali Ridge collections are longer glumes, slightly fewer tertiaries, a shorter sterile zone and a slightly higher Condensation Index, it seems probable that the Alkali Ridge maize in fact was slightly more Mexican-like than that from Floating House. The difference, if it really existed, was not at all extreme and no more than might be found to-day between the same variety of maize grown in two different Mexican villages.

It is not surprising to find that the maize from the two sites is so similar. They are not far apart in space and were apparently closely contemporaneous. This section of Floating House may be dated as belonging to Pueblo II or Pueblo III, and the Alkali Ridge material as Pueblo I or II. This means that the two sets are within a few hundred years of each other at the most and around 1000 A. D., according to the most widely accepted chronology for the Southwest. Bryan⁴ summarizes current opinions on southwestern chronology as follows:

| | |
|-----------------|-----------|
| "Pueblo V | 1600 |
| Pueblo IV | 1300-1600 |
| Pueblo III | 1100-1300 |
| Pueblo II | 900-1100 |
| Pueblo I | 700- 900 |
| Basketmaker III | 500- 700 |

³ Anderson, *loc. cit.*

⁴ Ann. Assoc. Am. Geogr. 31:p. 9.

Basketmaker II _____ ? - 500

Basketmaker I _____ postulated

Various authorities use slightly different dates, and some question the reality of the boundaries between some of the categories."

The evidence reported above will have greater significance when it can be seen against a background of exact comparisons with various prehistoric and modern collections from the same general area. However, it is in harmony with such facts as have already emerged. The few-rowed primitive flints of the early Basket Makers were apparently gradually tempered by many-rowed Mexican dents which diffused into the "fourcorners" region, *apparently from the north*. (The most extremely "Mexican" collections we have yet seen are those of Scoggins from Yampa Canyon, Colorado, which grade into a group from northern Utah, and the two tassel series described here show even further dilutions of the Mexican influence.) At a later date (1200-1300 A. D.) southwestern maize changed suddenly and radically when long-eared, crescent-seeded types spread into the region, apparently, either directly or indirectly, from the eastern United States⁵.

SUMMARY

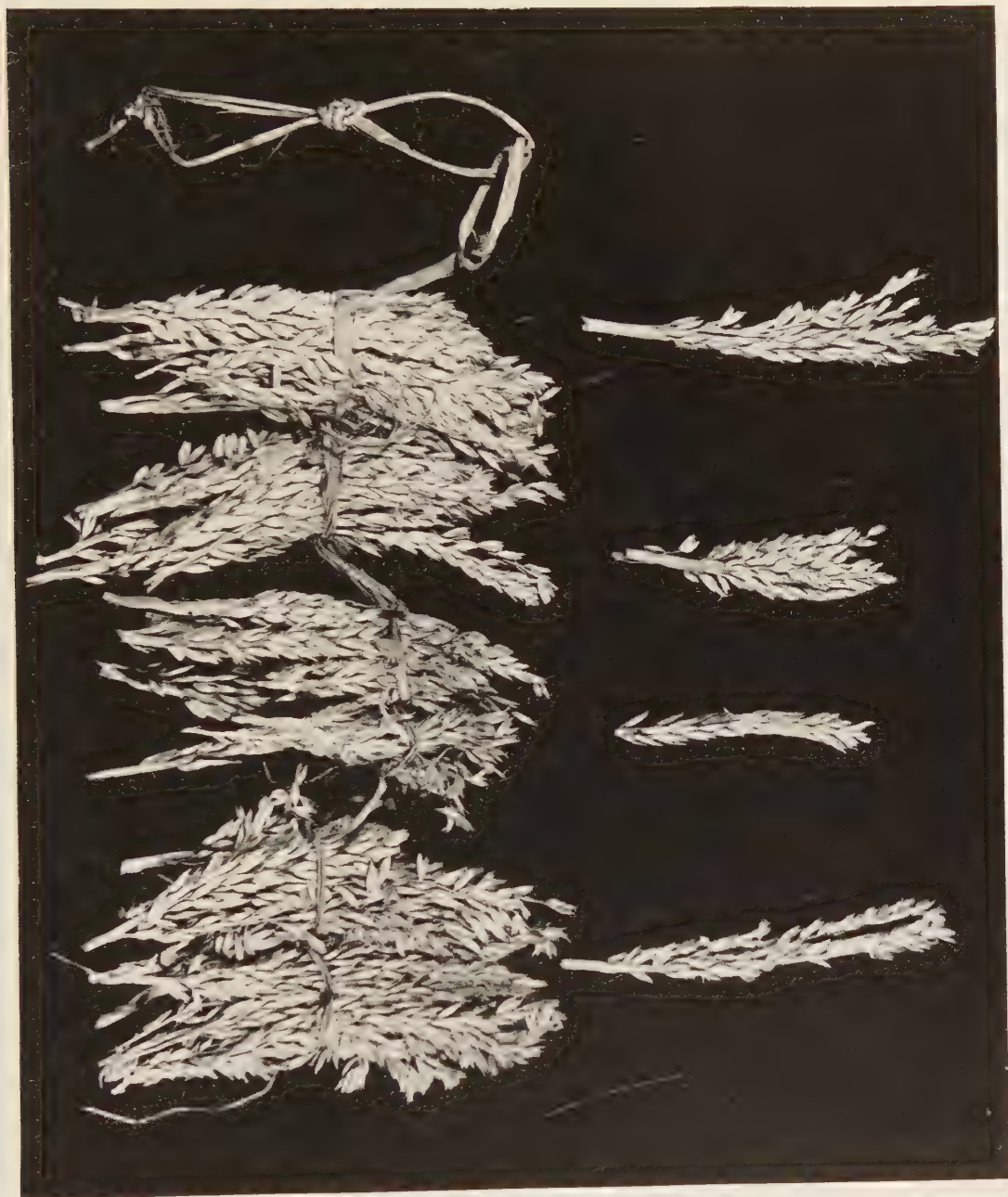
1. The importance of preserving tassels, as well as the ears, of prehistoric maize is illustrated by two collections from the Peabody Museum.
2. The chief features of a maize tassel are enumerated and methods of scoring the variation exactly are described and illustrated.
3. The tassels from Alkali Ridge were tied together with bark and had apparently been prepared for ceremonial use.
4. The two collections are very similar, the one from Alkali Ridge being slightly more Mexican in its technical characteristics. Both series have such slight plant-to-plant variation as to imply a high grade of agronomic skill on the part of their cultivators.
5. The collections are discussed briefly with reference to what is now known of the history of maize in the Southwest.

⁵ Carter, George F., and Edgar Anderson. Paper in press.

EXPLANATION OF PLATE

PLATE 18

Pre-Columbian tassels from Alkali Ridge, Utah. Peabody Museum, No. 33-44-10/3572. Photograph courtesy of the Peabody Museum, Harvard University.



EXPLANATION OF PLATE

PLATE 19

Tassel and tassel fragments from the band shown in pl. 18: Right: One of the most perfect tassels from the collection, this is scored in detail in text-fig. 2. Left: Fragments from two tassel branches; the upper contains no condensed internodes and the pedicellate spikelets are clearly shown; the lower fragment has sessile spikelets and a few condensed internodes.

Photograph courtesy of the Peabody Museum, Harvard University.



ANDERSON—PREHISTORIC CORN TASSELS

THE SOURCES OF EFFECTIVE GERM-PLASM IN HYBRID MAIZE

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The last twenty years have seen a complete change in the corn-breeding methods of the U. S. corn belt. Since 1924, when "Copper Cross" was first offered for sale in Iowa¹, hybrid corn has almost entirely supplanted open-pollinated varieties in that area. In the summer of 1944 one could drive across the state without seeing a single field of open-pollinated corn, and in order to find one of any size for study it was necessary to make an intensive search. The total annual yield of hybrid corn in the United States is now about two billion bushels, and the sale of the hybrid seed grosses well over fifty million dollars annually. These are matters of common knowledge to corn breeders but they need to be discussed in terms of population genetics, since the problems they raise are of theoretical as well as practical importance.

In terms of gene combinations and their distributions, the whole genetic pattern of *Zea Mays* in the United States has been catastrophically overhauled in the last two decades. To describe precisely what has happened to the maize germ-plasm of the U. S. corn belt and to predict its probable effects is a gigantic problem in population genetics. This paper is an attempt to look at the problem as a whole and to give it a preliminary discussion; to estimate some of the facts and to put them on record. Some of these facts are every-day matters to those in the seed-corn business, and it may seem trivial to record them. For some of the others even the estimates must necessarily be so controversial as to be scarcely more than one man's opinion. In gathering the information and discussing its significance I have relied almost wholly upon the staff of the Pioneer Hi-Bred Corn Company. Mr. Raymond Baker, the manager of the breeding department, and his assistants (Messrs. Karl Jarvis, Sam Goodsell, and James Weatherspoon) have put their knowledge and records at my disposal. They also took the trouble to locate Mr. Hershey and obtain the interviews reproduced below. I have done no more than to phrase the problem and to write the paper. If the conclusions, however, are out of line with the actual facts, the fault is entirely my own.

Before discussing gene-pattern distributions it will be necessary to describe the method of producing and marketing modern hybrid seed corn for those unfamiliar with the process. Maize is normally open-pollinated and the plants under such conditions are highly heterozygous. In producing hybrid corn, uniform inbred lines are produced by controlled self-pollinations or sib-pollinations until practical homozygosity has been reached (usually six or more generations). Most of the inbreds produced in this way are discarded or eliminate themselves by their sterility. The few which remain are tested in crosses with each other until sets

¹ Iowa Seed Co. Catalogue. 1924, p. 30.

of four inbreds are obtained which make an effective "four-way" cross. (Single crosses and top-crosses are also produced but the bulk of the business is now in four-way crosses.) Let us designate the four in any one cross as 'A', 'B', 'C', and 'D'. 'A' and 'B' are crossed together the first year in one plot (by detasseling, i. e., removing the male inflorescence from one parent) and 'C' and 'D' in another. The following year hybrid 'AB' is interplanted with hybrid 'CD'. The present practice is usually to have this done under contract by skilled farmers, who detassel either 'AB' or 'CD', as the case may be, and the resulting crop ('AB' x 'CD') is marketed as seed corn. A large part of the effort in modern corn breeding is spent in maintaining and improving the inbred lines upon which the business is based. In addition to the purely negative effort of roguing, the development of "Convergent Improvement" by Richey and Sprague² has resulted in what are termed in the trade as "second cycle" and "third cycle" inbreds. These are produced as follows: Let us suppose that inbred 'XYZ' is useful in a particular set of crosses except that it has certain obvious faults. It might, for example, have such weak roots or short ears that even its hybrid offspring are affected; or it might, on the other hand, be so weak as to be difficult to raise in quantity year after year. In a convergent improvement program 'XYZ' is therefore crossed with a series of other inbreds (or with an open-pollinated variety) and the resulting hybrids are backcrossed to 'XYZ' again. From these three-quarter bloods, by inbreeding and selection, a series of second-cycle inbreds is obtained, and if the work has been well done at least one of them may have most of the advantages of 'XYZ' without all of its defects.

Such is the present system. By it, effective gene combinations are discovered in the breeding plots of the experiment stations and corn-breeding companies and are propagated for sale to the actual farmer. Where did these gene combinations come from on the whole? Do they trace back to many open-pollinated varieties or to a few, and how does the present process of obtaining effective gene combinations compare with that in vogue before the hybrid-corn business came into being? To obtain an approximate answer to these questions 6 widely sold four-way hybrids of known composition were listed. They are all outstanding commercial successes and have been very widely planted. They might, in one year or another, have accounted for one-quarter of the total corn crop in central Iowa. Since all are four-way crosses we might have expected as many as 24 inbred lines; actually only 18 are involved, the inbreds known as Ill A, Iowa 205, R-4, Wf-9, and Ill-HY having entered into two or more crosses. When the 18 inbreds are tabulated according to the open-pollinated variety from which they were derived, we find the whole group came from only 3 open-pollinated varieties! Twelve are from some strain of Reid Yellow Dent, 3 from Krug, and 3 are from Lancaster Surecropper, as follows:

² Richey, Frederick D., and George F. Sprague. Experiments on hybrid vigor and convergent improvement in corn. U. S. Dept. Agr., Tech. Bull. 267:1-22. 1931.

REID YELLOW DENT: HY, 38-11, WF-9, Os 420, Os-426, Ia 205, R-4, Ill A, Idt, Ind Fe, TEA, LE-773.

KRUG: K-77, K-187, K-159.

LANCASTER SURECROPPER: L-317, L-289, LDG.

The way in which the inbreds are combined is also significant. The six four-way hybrids under consideration were combined as follows:

3 hybrids: 3 Reid inbreds and 1 Lancaster inbred.

1 hybrid: 2 Reid inbreds, 1 Lancaster inbred and 1 Krug inbred.

1 hybrid: 2 Reid inbreds and 2 Krug inbreds.

1 hybrid: 4 Reid inbreds.

The above estimate is from only one section of the corn belt but it is in line with what is generally known. The bulk of the inbreds now being most widely used were derived from very few open-pollinated varieties. In the above sample only 3 open-pollinated varieties were represented—Reid Yellow Dent, Lancaster Surecropper, and Krug. The last of these is little more than a sub-strain of Reid. According to Wallace and Bressman³, it was originated by George Krug of Woodford, Illinois, who crossed Gold Mine with a Nebraska strain of Reid and selected for a smoother rather small-eared utility corn.

We are faced with the remarkable fact therefore that much of the corn now being grown traces back mainly to two open-pollinated varieties. It is not surprising to find Reid inbreds high on the list since that variety in one sub-strain or another dominated the corn belt when hybrid corn was being evolved. Popularity might also help to explain the prevalence of Krug inbreds, this variety having been very extensively grown in the central corn belt immediately before the advent of hybrid corn on a commercial scale. However, these were by no means the only varieties grown commercially at that time. As late as 1906, when E. M. East was just starting his work with inbreeding, 11 varieties of yellow dent corn were offered for sale by the Iowa Seed Co. in Des Moines. The standard authorities on corn growing, Wallace and Bressman³, in 1937 listed the following open-pollinated yellow dents as commercially important in the central corn belt: Reliance, Leaming, Gold Mine, Ioleaming, Golden King, in addition, of course, to Reid and Krug. Some of these are known to have been inbred fairly extensively, yet only the Reid and Krug inbreds have held up under commercial competition. Popularity of the open-pollinated variety certainly would not explain the success of Lancaster Surecropper inbreds. This variety was of such minor importance in the corn belt that Wallace and Bressman merely list it among the "also-rans" without any further comment. It was not until its inbreds demonstrated their usefulness that it became a real factor there. Its excellence as a source of good inbreds is well known among corn-breeders. In addition to the inbreds listed above a number of other excellent ones have been derived in whole or in part from

³ Wallace, Henry A., and Earl N. Bressman. Corn and corn growing. New York. 4th ed. 1937 (see p. 208).

³ *loc. cit.*

this variety, and Dr. F. D. Richey informs me that at least three well-known inbred lines came from a single open-pollinated ear of Lancaster Surecopper. It is also generally appreciated that the inclusion of a Lancaster inbred in a four-way hybrid steps up productivity, and it will be noted that half of the hybrids listed above were so constituted.

It is apparently true therefore that the inbred strains in use at the present time are far from a random sample of the open-pollinated varieties which immediately preceded them. Many of the minor varieties of yellow dent are not represented by inbreds derived from them. The germ-plasm of two open-pollinated varieties predominates in modern inbreds, and one of these varieties, Lancaster Surecopper, is represented out of all proportion to its previous importance in this region. If these phenomena are general and not merely a chance result, they raise a number of interesting questions. A few of these can be suggested here: (1) If Lancaster Surecopper is really an especially effective source of good inbreds is there anything in its history to suggest why this might be so? (2) How do the frequency and the pattern of effective gene combinations in hybrid maize compare to those in the open-pollinated varieties? How much of the apparent progress is merely the uncovering of progress already achieved by the originators of Reid, Krug, and Lancaster Surecopper? Is potentially effective germ-plasm being lost under the present system?

To question number 1 we can give a partial answer. Lancaster Surecopper was originated in Pennsylvania by Mr. Isaac Hershey and his father. The former is still living, and Mr. Karl Jarvis and Mr. James Weatherspoon of the Pioneer Hi-Bred Corn Company visited him in September of this year and have kindly prepared accounts of the interview. Mr. Jarvis's is printed in its entirety; supplementary and confirmatory evidence from Weatherspoon's report is given in brackets:

In 1860 (when Isaac Hershey was eight years old) a neighbor, Henry High of Byers-town, Lancaster Co., Pa., received a packet of a variety of corn from the Patent Office. Mr. High and several of the neighbors liked this new variety and some of them, especially Jacob Hershey (Isaac Hershey's father) and Jacob's brothers, began to depend on it for their main crop. It was described as a rather small, rather slender-eared corn, very variable in type [but a good yielder]. In general, it was rather smooth, mainly one-eared, and rather early. From Mr. Hershey's description I got the impression that it must have been either a semi-flint or else a flint-dent hybrid which was still segregating. One of the common segregates was a "lilac colored" ear, which caused one of Isaac Hershey's uncles to nickname it "Lilac corn."

The common corn of the community was a large, late, rather coarse type with medium to rough kernels, rather resembling Golden Queen according to Mr. Hershey. The new variety, "Lilac corn," was such a contrast and looked so much smaller, even though very productive, that most farmers laughed at it and called it "popcorn." The Hersheys began selecting later strains and blending in a little seed from a few selected ears of the larger, later and rougher local varieties. This blending process, which Isaac Hershey called "dipping," was repeated a number of times [by his father] before Isaac started farming, but he does not know just how many times. Isaac estimated that he himself had "dipped" Lancaster Surecopper six or eight times with various varieties including once with some white corn. "Dipping" consisted of taking two or three selected, high-yielding ears, shelling them, and then mixing the seed thoroughly throughout his pile of shelled seed corn. The last dip was about 1910.

One year, Isaac Hershey planted a field to Golden Queen. The stand was very poor so he replanted with Lancaster Surecopper. Since he saved some seed corn from this field, he undoubtedly introduced considerable Golden Queen into his variety. In addition, after his neighbors began to get seed from him and then grow their own strains, Isaac Hershey would watch their fields and when a strain had been carried on for eight to ten years and seemed to be desirable, he would buy back about one-half bushel of selected seed and blend it into his own.

At first there was no attempt to make the variety uniform. In fact, if anything, they (Isaac and Jacob, and Noah, son of Isaac) preferred to keep it "mongrelized." In seed selection, in general, he preferred a medium-length ear, but would save any ear irrespective of type which was, as he said, "a good business ear that would put lots of pork on a hog." He insisted on well-matured, sound ears with clean shanks and no mold or "silk cut." He said he could recognize the latter by slightly protruding kernels. This insistence on a sound, well-matured ear earned it the name of "Surecopper," since it always matured while other later, softer varieties did not. [He did pick ears with good solid, clean shanks, evidently ears with a reasonable amount of length. In regard to length, he did say this—that he kept an ear for seed if it was somewhat short, provided that the kernels were not filled out clear over the end. He seemed to think if there was still bare cob sticking out at the end the ear still had considerable chance to develop more length. However, if it was a short ear and filled out to the end, he believed there wasn't any possibility of getting any length out of it.] No plant type selection was made because, "I never saw a good ear of corn on a poor corn plant." His only regret was that this type of selection had given a weak-rooted variety. However, his son, Noah Hershey, had later selected for a larger ear and a better root system by making field selections.

When Lancaster Surecopper became popular and seedmen began buying seed from Mr. Hershey, they continually put pressure on him to select for uniformity and a longer, more showy ear type. He refused at first, but finally gave in, and, as he said, "spoiled Surecopper and cut off about 10 to 15 bushels per acre at least." This "spoiling" occurred about 30 years ago. Some years ago Pennsylvania State College asked him to select a sample of Lancaster Surecopper representing the original range of types as he originally grew the variety, before he "spoiled" it. This was done and sent to them and may possibly still be stored somewhere at State College. [In the early days with the development of Lancaster Surecopper, Hershey didn't go in for selling seed very much. He was mostly interested in a high-yielding corn. However, as the fame of his corn spread seedmen wanted to sell Lancaster Surecopper, but they, of course, insisted that he dress the corn up—that is, select for uniformity of ear type. So, along about 1910, he began to sell quite a bit of seed and he stopped "dipping" his corn and began to select for uniformity. He feels very strongly himself that at this stage he began spoiling his corn. In fact, he said that he wrote to a worker in the U. S. D. A. and told him how he spoiled Lancaster Surecopper, and that was by selecting for uniformity as to ear type and dressing it up to suit the seedsmen.]

Incidentally, Mr. and Mrs. Hershey mentioned as a very profitable year one in which they sold 1,000 bushels of seed at \$3.00 per bushel. For super-select seed such as he himself would plant, the charge was \$5.00 per bushel. Since ordinary corn was bringing 50 to 60 cents per bushel at that time, they were very glad to get such prices. At various times Lancaster Surecopper was shipped to Europe, China and frequently to South America so its germ-plasm may well be scattered throughout the world.

Mr. Hershey's opinion of the bad effects of selection for uniformity is interesting because it parallels conclusions reached from a morphological study of recombination in species crosses⁴. From both theoretical and experimental considerations it was shown that the achievement of optimum recombinations in crosses between species or races is a difficult and long-time affair. Relatively little progress can be made in any one generation. The practical problem involved is to be able to work towards the desired end, generation by generation, without losing potentially valuable genes before they are incorporated with the other superior ones. In the paper referred to, it was suggested that simultaneous selection for performance and for morphological diversity might solve this dilemma. It is interesting to find that a family of successful corn-breeders has come to

⁴ Anderson, Edgar. Recombination in species crosses. *Genetics* 24:668-698. 1939.

rather similar conclusions on the basis of practical experience. It should be possible to test these conclusions experimentally. Parallel convergent improvement experiments⁵ could be set up with and without selection for morphological diversity during the generations of selection and inbreeding. If Mr. Hershey and I are right a more complete synthesis of desirable genes could be achieved by considering the general morphology of the plants chosen as parents in each generation as well as their performance. (See Anderson, *loc. cit.*, pp. 694-695, for a more complete discussion.)

The second set of questions (concerning the pattern of gene combinations) cannot be answered at the present time, nor have I found any general unanimity of opinion among maize breeders or maize geneticists. We know virtually nothing about the breeding structure (or, to put it in other words, the population genetics) of a field of maize. On this fundamental subject almost nothing has been written. The title of Shull's pioneer paper⁶ defined the problem but his discoveries helped to initiate four decades of more pressingly practical research. Jones and others have shown that mating is not at random in open-pollinated fields⁷. One can scarcely visit a maize-breeding farm without noticing a number of very suggestive phenomena which bear on the problem, yet at present we are almost without facts. We do not even have a simple plant-by-plant description of a single field of any open-pollinated variety, let alone an estimate of how the individuals of one generation are related genetically to those of the next. Yet before we can give reasoned answers to such questions as those raised above, we must have fairly reliable estimates on these matters.

To achieve optimum results with hybrid-corn breeding we must understand at least approximately the population genetics of a field of open-pollinated maize. We shall have to move swiftly if the desired information is to be recorded; open-pollinated fields are almost a thing of the past. It may be necessary for breeders of hybrid corn to subsidize highly skilled farmers as raisers of open-pollinated corn until we have at least an estimate of when, where, and how the majority of the useful gene combinations in hybrid corn were accomplished.

SUMMARY

1. An attempt was made to determine which open-pollinated varieties of maize have contributed most germ-plasm to modern four-way hybrids.
2. For central Iowa it was shown that one group of highly successful hybrids was made up wholly of inbreds from three open-pollinated varieties, Reid, Krug, and Lancaster Surecopper.
3. Evidence is given for the particular excellence of this latter variety as a source of hybrid germ-plasm. The history of the variety was obtained from Isaac

⁵ Richey and Sprague, *loc. cit.*

⁶ Shull, George H. The composition of a field of maize. *Amer. Breed. Assoc. Rept.* 4:296-301, 1908.

⁷ Jones, D. F. Selective fertilization. 163 pp. Chicago. 1938.

Hershey, one of the originators, and his methods of selection are described.

4. Two questions are discussed in the light of the above information: (a) the possible advantages of selecting simultaneously for performance and morphological diversity; (b) the need of more exact information on population structure in *Zea Mays*. It is concluded that, for the sake of understanding and improving modern hybrid maize, it will be necessary to investigate the breeding structure of representative open-pollinated varieties.

NOTES ON SOME NORTH AMERICAN ASCLEPIADS

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For nearly ten years I have been engaged more or less actively in a revision of the species of *Asclepias* in the United States. The problem has been complicated and its completion delayed by a number of factors, particularly the need of delineation of the genus with respect to the other American genera of Asclepiadaceae. World War II brought its own complications, all too familiar to any systematist, in this case the chief of which was the enlistment in the "Seabees" of Albert A. Heinze, long my collaborating illustrator. With the indefinite duration of these hindrances in mind, I have thought it best to publish occasional novelties; I now offer some notes concerning the nomenclature and identity of a few of our North American Asclepiads, not only because they should have been discussed long ago, but because I intend to publish in the near future some observations on their geographical variation.

ASCLEPIAS MEXICANA HBK. VS. *A. FASCICULARIS* DCNE.

One of the most frequent Milkweeds of our western states is "*Asclepias mexicana*" of nearly all American authors, which ranges roughly from Idaho to Nevada and westward to the Pacific Coast. It is a member of the *incarnata*-alliance of the subgen. *Euasclepias*, having narrowly stipitate gynostegia, whorled leaves, and paired or clustered inflorescences at the upper nodes. The flowers are grayish-pink to white, and, as is usual in this alliance of the subgenus, offer few structural peculiarities indeed, the only one coming to mind at the moment being the attachment of the corona horn usually at the middle, rather than at the base, of the hood.

Apparently the best diagnostic characters of the species, again as is usual in its alliance, are found in the leaf-branch system. The phyllotaxy is particularly notable, that upon the main stem and flowering branches being predominantly ternate, but occasionally quaternate or even opposite. In addition to the flowering branches of normal size, the species is distinguished usually at a glance by means of dwarf axillary branches which do not flower as a rule and lend to the plant a somewhat "heterophyllous" aspect because of their usually smaller, predominantly opposite leaves. In any case, the stems and branches are either glabrous or inconspicuously and generally pubescent, without the appearance of pubescent "lines" which will be discussed presently in other connections. This species may well extend northward into southern British Columbia and southward into Baja California, although the herbarium of the Missouri Botanical Garden has no supporting evidence.

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"*Asclepias mexicana*" of the western United States invariably is credited to Cavanilles (Ic. 1:42. pl. 58. 1791), and an examination of the original description and illustration alone might not appear to bar such an interpretation. The former, as one might fear, is somewhat vague, and conveys as its most important clues that the leaves of the plant are whorled and about three inches long by three lines broad. The illustration is rather conventional in the antique manner, and shows 5-6 lance-elliptic leaves in a close whorl, without axillary branches, and with highly generalized inflorescences. No locality is cited by Cavanilles, although a majority of his Mexican species are known to have been collected in the mountainous districts in the vicinity of Mexico City (as in the case of *A. Linaria*, "*prope Mexico et Chalco*"), and there is some justification for the assumption that his *A. mexicana* might well have been from the same region.

As a matter of fact, this assumption virtually is proved by the Mexican *exsiccatae* labelled "*A. mexicana* Cav.," a fair number of which occur in American herbaria. Attention is first directed to such specimens in the herbarium of the Missouri Botanical Garden when it is noted that they came not from districts contiguous to the distribution of "*A. mexicana*" in the western United States, but from the southern and eastern Mexican states of Nuevo Leon, Mexico, Oaxaca, and the Distrito Federal. Comparison with the large suites of the West Coast "*mexicana*" proves the two populations to represent distinct species.

The Mexican species at first glance is of a much "neater" habit, and upon only one specimen of the nine before me is there any indication of the dwarf axillary branches so characteristic of the West Coast species. The leaves are in much closer, more uniform whorls of 4, or very rarely 5, never 3, individuals, and they are of somewhat coriaceous or fleshy texture as evidenced by their revolute margins, a character that I have never observed in the plants of the United States. The stems of the Mexican species may be glabrate below, but in the upper portion they are marked by four pubescent lines decurrent from the bases of the leaves. The importance of these lines will be stressed further in another connection. The flowers of the Mexican species are disappointingly similar to those of the western United States, as might be expected, and the only technical distinction that I have noted is a strong tendency for the corona horns of the Mexican species to be inserted at the base of the hood, whilst they are inserted at about the middle in the species of the United States.

After such considerations, a return to Cavanilles' plate will convince most readers that the pioneer Spanish botanist had before him, in fact, not the species of the western United States, but that of southern and eastern Mexico! Nor is one in want of a name for the northern species, for *A. fascicularis* Dcne. (in DC. Prodr. 8:569. 1944), based upon a collection by Douglas (in "*Nova California*"), immediately is available, although the original description, again, is quite non-committal. In "*New California*" Douglas could have collected but one Milkweed with verticillate leaves.

ASCLEPIAS GALIOIDES HBK. VS. A. SUBVERTICILLATA (GRAY) VAIL

Because of its poisonous properties, stockmen throughout the western plains of the United States, from Nebraska to Texas and westward to Idaho and Arizona, usually are familiar with the plant widely known as "*Asclepias galioides* HBK.". This species closely resembles the frequent *A. verticillata* L. of the East from which it is distinguished, occasionally with some difficulty, by means of its more extensive taproot system and tendency to the production of dwarf, microphyllous, axillary branches similar to those of the closely related *A. fascicularis* Dcne. As in the latter species also, the leaves of this plant are predominantly ternate, but occasionally 4-5-nate or opposite, particularly above and upon the microphyllous dwarf shoots. Because of the variability of the leaf whorls, Dr. Gray proposed for certain of these plants the name *A. verticillata* var. *subverticillata* (Proc. Amer. Acad. 12:71. 1876), which was raised to specific rank by Miss Vail in 1898 (Bull. Torrey Club 25:178). In my studies I have made every effort to distinguish *A. subverticillata* from the commonly recurrent "*A. galioides*", but, because of the general variability of the population as a whole, have come to the conclusion that they are not even varietally distinct.

Asclepias galioides, as originally described by Kunth (HBK. Nov. Gen. & Sp. 3:188. 1819) was based upon a Mexican plant collected "*inter Valladolid de Mechoacan et lacum Cuiseo*" (Bonpland 4304 in Hb. Paris or Berlin), which is unavailable to us at present and may be permanently lost. No illustration accompanies the text, and the description as a whole is scarcely definitive with the exception of the brief introductory diagnosis: "*A. caule suffruticosa, ramoso, quadrifariam piloso; foliis quaternis, subsessilibus, erectis, linearibus, margine revolutis, uninerviis, glabris, . . . folia . . . 2-2½ pollices longa, 1-1½ lineas lata.*"

Here, at least, is a definite geographical citation, from the highlands of Michoacan, with a critical description of the stem and foliage. If we now turn to the herbarium of the Missouri Botanical Garden, we find that there are two elements amongst the Mexican specimens labelled as "*A. galioides*." More numerous are plants from the north-central plains and foothills of Chihuahua, Coahuila, Durango, and northwestern San Luis Potosi, which agree perfectly with the plants of the adjacent plains of the United States, having predominantly ternate leaves 0.1-0.3 cm. broad and stems which are either glabrous or with two decurrent lines of pubescence. But amongst the lot are three specimens from the high Sierra Madre Oriental of Nuevo Leon (Muller & Muller 248), San Luis Potosi (Parry & Palmer 584), and Mexico (Hahn s. n.) which obviously would have been distributed as *A. mexicana* but for their quaternate slightly narrower leaves (0.2-0.5 cm. broad), and stems which also show plainly the four pubescent lines characteristic of typical *A. mexicana* as represented by our collections, and as noted by Kunth. Since a "Paris line," probably intended by Kunth, equals 2.325 mm., it is fairly obvious that the true *A. galioides* HBK. is only an intergrading

narrow-leaved phase of *A. mexicana* Cav., the lance-elliptic leaves of which vary from 0.3 to 1.0 cm. broad upon the basis of our present representation. The proper designation of "*A. galioides*" of the plains of the west-central United States and adjacent north-central Mexico, therefore, is *A. subverticillata* (A. Gray) Vail.

THREE SUBSPECIES OF ASCLEPIAS TUBEROSA

One of the most beautiful and familiar Asclepiads of the United States is the commonly orange-flowered Butterflyweed, the inclusive species *A. tuberosa* L., which ranges roughly from Massachusetts to peninsular Florida and westward to Colorado and Arizona. The plants commonly assigned to *A. tuberosa* are notoriously variable, and it is not unnatural that there are two opposed views concerning them.

The less conservative view is that of the late Dr. John K. Small, who was able to recognize three specific entities in the complex and keyed them as follows in his 'Flora of the Southeastern United States' (ed. 1, p. 941. 1903):

- | | |
|--|------------------------|
| Hoods linear-oblong or linear-lanceolate, the interior folds meeting the margins near the apex; calyx-lobes barely $\frac{1}{3}$ as long as the corolla-lobes. | |
| Leaf-blades oblong, obtuse: follicles slender-fusiform..... | 1. <i>A. decumbens</i> |
| Leaf-blades lanceolate-oblong or linear-lanceolate, acute or rarely obtuse; follicles fusiform..... | 2. <i>A. tuberosa</i> |
| Hoods broadly oblong, the interior folds vanishing remote from the apex; calyx-lobes nearly $\frac{1}{2}$ as long as the corolla-lobes..... | 2a. <i>A. Rolfsii</i> |

In the text, Dr. Small indicated the distribution of *A. decumbens* L. as, "In dry fields, New York, Ohio and Illinois to North Carolina and Florida. Occurring also probably elsewhere further north"; that of *A. tuberosa* L. as, "In dry fields, Maine to Ontario, Minnesota, Colorado, Florida, Texas and Arizona"; and that of *A. Rolfsii* Britton as, "In pine lands, southern peninsular Florida."

The second edition of Small's 'Flora' treats the complex precisely as in the first. However, his 'Manual of the Southeastern Flora' (p. 1068. 1933) presents a surprisingly different key for the same three species:

- | | |
|--|------------------------|
| Leaf-blades acute or acutish, lanceolate or lance-elliptic: horn very slender. | |
| Calyx-lobes $\frac{1}{3}$ the length of the corolla-lobes or less: hood narrowly elliptic..... | 1. <i>A. decumbens</i> |
| Calyx-lobes nearly as long as the corolla-lobes: hoods obovate..... | 2. <i>A. tuberosa</i> |
| Leaf-blades obtuse and broadly rounded, pandurate; horn very stout..... | 3. <i>A. Rolfsii</i> |

The distributions are somewhat altered as follows: for *A. decumbens*, "Dry fields, various provinces, Fla. to Tex., Ill., and N. Y., probably also further north"; for *A. tuberosa*, "Dry fields, various provinces, Fla. to Tex., Ariz., Minn., Ont., and Me."; and for *A. Rolfsii*, "Pinelands, Coastal Plain, Fla. to S. C.". Perhaps the chief impression to be received from Dr. Small's two treatments of our problem might be summarized as considerable uncertainty regarding morphological criteria, and suspiciously coincident geographical distributions, particularly of *A. decumbens* and *A. tuberosa*.

The more conservative view of the *A. tuberosa* problem recently has been expressed very forcibly in a letter to me by Professor M. L. Fernald, which I wish to quote:

"In my own work and in the treatment of the genus for the Manual, I have found it impossible to draw any geographic or morphological lines in *A. tuberosa* except for possibly minor forms. The type, of which I have a photograph, of *A. tuberosa*, that is, the specimen in the Linnean Herbarium when he prepared Species Plantarum and which was marked by him K [Kalm] *tuberosa*, has oblong leaves broadly rounded or auricled at base and somewhat clasping. We have no photograph of the type of *A. decumbens*, but that was a Virginian plant, presumably based on a Clayton specimen (Gronovius) from a region where Clayton could have collected almost anything in the group.

"As I look over our material, and as I know intimately the plant in eastern Virginia, it is heteromorphic, and one can get any color that he wishes to collect, from the ordinary plant with vivid orange hoods and reflexed carmine perianth to others with the hoods red, and others with them pale to bright yellow, and others with hoods and perianth bright yellow. These color-variations which are helter-skelter, occur on plants with strongly ascending stems or others with the stems lopping while the leaves may be anything from broadly rounded at base and subclasping to subcuneate at base in the same or adjacent patches. They may be narrowly ovate, narrowly oblong, oblong- or linear-lanceolate, round-tipped or acute and, as I said, I have personally abandoned all hope of getting any tangibility into the series. It is certainly not divisible into one lot growing (as you express it) north and west of the Ohio, as contrasted with others growing farther south and east, for on the coast from New England southward we can find plenty of specimens with broad-based leaves to match the most extreme plants farther west, while from Michigan, Indiana, or Minnesota we can find plenty of specimens with the leaves as narrow and oblong as in the more extreme plants of the Atlantic states.

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"Certainly the type of *A. tuberosa* is easily matched both east and west. Coming from Kalm, it naturally did not come from north or west of the Ohio, but presumably from New Jersey or eastern Pennsylvania, for Kalm had his headquarters in that vicinity. And *A. decumbens*, if it was anything more than a form, was from decidedly an eastern area, where anything within the group can be found."

Professor Fernald refers to my view expressed in a previous letter to him soliciting his opinion, which was freely given as quoted. My observation had been, simply put, that the leaves of *A. tuberosa* from roughly north of the Ohio and west of the lower Mississippi Rivers are generally broadest below the middle, while those east and south tend to be broadest above the middle, although this population also contains many of nearly oblong or elliptic outline. The western population also may be said to have the leaf base predominantly truncate or cordate, while the eastern population varies from narrowly cuneate to somewhat cordate, as Professor Fernald testifies. In Florida, a third population occurs, currently known as *A. Rolfsii*, in which the leaves tend to be broadest above the middle, but usually more or less conspicuously hastate at the base, although rarely cuneate as in the more northern plants.

In the material of *A. tuberosa* generously lent for my study by the Gray Herbarium, I was very interested to find a sheet from the herbarium of Dr. Gray upon which are pasted two separate collections in the manner commonly employed in former times. The specimen to the right was collected by Oakes at Plymouth, Mass., and shows the oblong-oblongate, broadly acute leaves to good advantage; the specimen to the left was collected by an unspecified person at Columbus, Ohio, and shows the broadly ovate-lanceolate leaves commonly found in the Midwest. In the extreme lower left corner of the sheet, Dr. Gray had affixed a label bearing the annotation "*Asclepias tuberosa* L.", and another label directly beneath the plant from Ohio bears the designation "var. *decumbens*". The latter annotation can have little claim to validity as typifying the proper nomenclature for the western population, since *Asclepias tuberosa* var. *decumbens* (L.) Pursh (Fl. Amer. Sept. 1:182. 1814) indisputably was provided for Virginian plants "with the

stems lopping" as discussed by Dr. Fernald in his letter.

It should be emphasized that the three populations noted by me are radically different from the three of Dr. Small in that their ranges do not overlap extensively, much less coincide. Furthermore, I have not been able to observe any significant morphological characters distinguishing the three species as noted by Small; his calyx lobe-corolla lobe ratios particularly have proved to be unreliable. The problem as I see it principally concerns leaf variation.

At this point we should examine the basic nomenclature of the three populations that I have observed. That of *A. Rolfsii* may be disposed of easily, since it is a modern species based upon a specimen deposited in the herbarium of the New York Botanical Garden and collected by the late Dr. N. L. Britton at Miami, Fla. This plant bears the more or less hastate leaves characteristic of the vast majority of the peninsular population. Concerning the Linnaean *AA. tuberosa* and *decumbens*, I can best refer again to Professor Fernald's letter, since the receipt of which I have been allowed to examine the photograph he mentioned. The leaves of this "type" of *A. tuberosa* in all respects are similar to those of the eastern population as a whole, being oblong-oblancoate, distinctly widest above the middle, broadly acute to obtuse at the tip, and gradually tapering to a narrow truncate or obscurely auriculate base. Professor Fernald's observations concerning the variability of the stem posture of the eastern population are particularly valuable in disqualifying that specific character ascribed to *A. decumbens* by Linnaeus.

All this, of course, leaves the western population without a specific name, unless I again have overlooked an obscure reference in Rafinesquiana. Nor do I find an appropriate varietal designation, although a few adjectives for color-forms have been proposed. I am proceeding to describe all three populations as subspecies, a category in great disuse if not misuse amongst contemporary plant systematists.

ASCLEPIAS TUBEROSA ssp. *tuberosa* Woodson, nom. nov.

Asclepias tuberosa L. Sp. Pl. 217. 1753.

Asclepias decumbens L. loc. cit. 216. 1753.

?*Asclepias revoluta* Raf. Fl. Ludov. 51. 1817.

Asclepias Floridana Lam. Encycl. 1:284. 1783.

Asclepias tuberosa var. *flexuosa* James, in Bot. Gaz. 13:271. 1888.

Acerates Floridana (Lam.) Hitchc. in Trans. Acad. Sci. St. Louis 5:508. 1891, as to name-bringing synonym only.

ASCLEPIAS TUBEROSA ssp. *Rolfsii* (Britton) Woodson, stat. nov.

Asclepias Rolfsii Britton, apud Small, Fl. Southeast. U. S. ed. 1. 943. 1903.

ASCLEPIAS TUBEROSA ssp. **interior** Woodson, ssp. nov. Plantae speciei habitu inflorescentiaque congruentes, in regione typica i. e. praecipue in planitiebus centro- et austro-occidentalibus foliis basim versus plus minusve latioribus semper ferme varie ovatis vel lanceolatis apice sensim acuminatis basi plerisque plus minusve cordatis vel non rare truncatis, ad regionem orientis i. e. prope fl. Ohiense et Mississipiense inferiore regioni ssp. *tuberosae* adjacentes ibique foliis saepe fere

oblongis vel ellipticis apice acutis nisi fere obtusis basi minus frequenter cordatis non rare fere cuneatis. — Exemplum typicum: IOWA: CLAY: level moist prairie six miles north of Ruthven, Sept. 4, 1944, *A. Hayden 3195* (Herb. Missouri Bot. Gard., *TYPE*).

Although intergrading specimens will constitute a recurring nuisance, as is to be expected in subspecies occupying contiguous ranges, the following key should be of some help in identifying specimens of the three subspecies:

Leaves typically obovate to linear-oblongate, i. e. broadest above the middle, intergrading to oblong and elliptic, particularly westward, the apex chiefly broadly acute to obtuse or rounded, the base cuneate or rounded, infrequently truncate or somewhat cordate, predominantly more or less conspicuously hastate in Florida and adjacent territory; Appalachian Mountains eastward and southward to the Coast, westward roughly to the Ohio and lower Mississippi Valleys.

Leaves uniformly rounded or cuneate toward the base from above, or infrequently about, the middle, the margins essentially flat or somewhat revolute; distribution cited above, except Florida in general.....ssp. *tuberosa*

Leaves predominantly with a more or less conspicuous hastate dilation toward the base, infrequently abruptly truncate, cordate, or essentially cuneate, the margins commonly more or less crisped; Florida and closely adjacent territory.....ssp. *Rolfii*

Leaves typically ovate to oblong-lanceolate, i. e. broadest below the middle, intergrading to oblong and elliptic, particularly eastward, the apex chiefly acuminate or narrowly acute, the base truncate or cordate, the margins flat or somewhat revolute; Arizona, southern Utah, and eastern Colorado to southern Minnesota and eastward to the Ohio and lower Mississippi Valleys.....ssp. *interior*

I have accumulated a considerable mass of statistical data which I intend to publish elsewhere, and which I have no doubt will constitute a convincing proof of the genetic significance of the three subspecies. The category of subspecies has been employed because the data obtained indicate that when graphically presented the character scores will coincide satisfactorily with the "continuous stepped cline" distinguished by J. S. Huxley (Bijdr. Dierk. 27:491. 1939) for numerous subspecies of animals. Huxley's "clines" undoubtedly will be found valid, if not extensible, when that method is applied widely to plant populations. I should explain further that I have decided to follow a suggestion of Huxley (in 'The New Systematics', Oxford, 1940, p. 37) regarding the treatment of two or more intergrading populations: thus I have labelled intergrading specimens, particularly in the Ohio and lower Mississippi Valleys, as "*Asclepias tuberosa* cl. *tuberosa-interior*," the abbreviation denoting the word "cline." I consider that this form of label is convenient, approximates biological reality, and is far more satisfactory than arbitrarily to assign an intergrade either to *A. t. tuberosa* or to *A. t. interior*. This method doubtless may be used in the case of intergrading varieties as well.

(To be continued)

EXPLANATION OF PLATE

PLATE 20

Asclepias tuberosa ssp. *tuberosa* and *A. tuberosa* ssp. *interior*. Explanation in the text.



WOODSON—SOME NORTH AMERICAN ASCLEPIADS

THE LILIACEOUS GENUS *Polygonatum* IN NORTH AMERICA¹

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A cytotaxonomic study of the North American species of *Polygonatum* was begun by the writer in 1935 at the suggestion and under the direction of Dr. Edgar Anderson and Dr. J. M. Greenman. Most of the work was completed within the next three years. Publication was delayed, however, because there still remained several involved problems, and it was hoped that additional field study might provide answers to some unsettled questions. It now seems desirable, in view of recent publications on the group, to present the conclusions to date and to point out some of the problems yet to be solved.

HISTORY

The generic name *Polygonatum* is derived from the character of the rhizome and is explained by Miller² as follows:

"so call'd of *πολὺ much*, and *γονὺ a Knee*, because it has many little Knees, for the Root is very knotty; It is also call'd *Solomon's-Seal*, because the Knots of the Root somewhat resemble a Seal."

The first use of the name *Polygonatum*, subsequent to the publication of Linnaeus's 'Species Plantarum' in 1753, was by Miller in the 'Abridgement' from 'The Gardener's Dictionary', published in 1754.³ Linnaeus⁴ listed three species of *Polygonatum* under the genus *Convallaria*, namely, *C. verticillata*, *C. Polygonatum* and *C. multiflora*. These were treated under the generic name *Polygonatum* by Allioni in 1785.⁵ The specific epithet of *Convallaria Polygonatum*, however, was changed to *officinale*. Thus, in accordance with the International Rules of Botanical Nomenclature, the name of the type species (*Convallaria Polygonatum* L.) becomes *Polygonatum officinale* All.

The first American species mentioned in literature is *Convallaria biflora*, described by Walter⁶ in 1788. In 1797, Poiret⁷ described *C. birta* Bosc, a species

¹ An investigation carried out at the Missouri Botanical Garden in the graduate laboratory of the Henry Shaw School of Botany of Washington University. A preliminary report was submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Science.

² Miller, Philip. The Gardeners Dictionary, ed. 1. 1731.

³ See Druce, G. Claridge. The abridgement of Miller's Gardener's Dictionary of 1754. Bot. Exch. Club & Soc. Brit. Isles Rept. 3:426-436. 1914, for a detailed account of this 'Abridgement', which seems to have escaped the notice of many botanical writers.

⁴ Linnaeus, C. Species plantarum, ed. 1. 1:315. 1753.

⁵ Allioni, Carlo. Flora pedemontana 1:130. 1785.

⁶ Walter, Thomas. Flora caroliniana, p. 122. 1788.

⁷ Poiret, J. L. M., in Lamarck, Encyclopédie méthodique. Botanique 4:369. 1797.

with hispid stems and pubescent leaves, said to have been sent from North America by Crevecoeur. However, no North American species with hispid stems is known to present-day botanists. In 1803, Michaux⁸ united all of the American species with the European *C. multiflora*. Willdenow,⁹ in 1806, described *C. pubescens* and *C. canaliculata* Mühl. In 1814, Pursh¹⁰ transferred all these species to *Polygonatum*, but changed the name *biflora* of Walter to *angustifolium*. He also added the European *P. latifolium* to his list of North American species. Poiret,¹¹ in 1816, described *Convallaria parviflora*, another species of doubtful affinities. Schultes¹² added *C. commutata* in 1830, and Dietrich¹³ proposed *Polygonatum giganteum* in 1835. In 1839, Hooker¹⁴ referred all of his American specimens to *P. multiflorum* β . *Americanum*. Torrey,¹⁵ in 1824, had recognized five species under *Convallaria*, but in 1843, he, too, referred them all to the European *P. multiflorum*.¹⁶ Wood,^{17, 18, 19} in the several editions of his 'Class-book of Botany' and in his 'American Botanist and Florist', considered the American species successively as varieties of *P. multiflorum* and of *P. biflorum*. In 1906, Greene²⁰ proposed three more species for the list, namely, *P. cuneatum*, *P. virginicum* and *P. boreale*. The New Mexican species was described by Wooton and Standley²¹ as *Salomonina cobrensis* in 1913. Recent editions of Gray's 'Manual'²² and Britton and Brown's 'Illustrated Flora'²³ recognize only two species, a pubescent one erroneously referred to as *P. biflorum*, and *P. commutatum* which includes the earlier *Convallaria biflora* of Walter.

More recent work on the genus has resulted in the description of numerous varieties and the making of various combinations. Farwell,²⁴ in 1915, reviewed the previous work on *Polygonatum*, divided the genus into two groups of species, the PUBESCENTES and the GLABRATA, and recognized in all five species and six varieties, several of which were proposed as new. In subsequent papers,^{25, 26, 27} he

⁸ Michaux, André. *Flora boreali-americana* 1:202. 1803.

⁹ Willdenow, Karl Ludwig. *Hortus berolinensis* 1:45, pl. 45. 1806.

¹⁰ Pursh, Frederick. *Flora americana septentrionalis* 1:234, 235. 1814.

¹¹ Poiret, J. L. M., in Lamarck, *Encyclopédie méthodique. Botanique. Suppl.* 4:29. 1816.

¹² Schultes, J. H., in Schultes & Schultes, *Systema vegetabilium* 72:1669-1671. 1830.

¹³ Dietrich, A., in Otto & Dietrich, *Allgemeine Gartenzeitung* 3:222, 223. 1835.

¹⁴ Hooker, W. J. *Flora boreali-americana* 2:176. 1839.

¹⁵ Torrey, John. *A flora of the northern and middle sections of the United States*, pp. 356, 357. 1824.

¹⁶ Torrey, John. *A flora of the state of New York* 2:299. 1843.

¹⁷ Wood, Alphonso. *Class-book of botany*, ed. 1, p. 396. 1845; ed. 2, p. 553. 1847.

¹⁸ Wood, Alphonso. *Class-book of botany; flora of the United States and Canada*, p. 714. 1861.

¹⁹ Wood, Alphonso. *The American botanist and florist*, p. 346. 1870.

²⁰ Greene, E. L. *Leaflets of botanical observation and criticism* 1:181, 182. 1906.

²¹ Wooton, E. O., and P. C. Standley. *Descriptions of new plants preliminary to a report upon the flora of New Mexico. Contrib. U. S. Nat. Herb.* 16:109-196, pl. 48-50. 1913.

²² Gray's *New manual of botany*, ed. 7. Revised by B. L. Robinson and M. L. Fernald, p. 292. 1908.

²³ Britton, N. L., and Addison Brown. *An illustrated flora of the northern United States, Canada and the British possessions*, ed. 2. 1:521. 1913.

²⁴ Farwell, O. A. *Notes on the Michigan species of Polygonatum. Bull. Torr. Bot. Club* 42:247-258, pl. 12-18. 1915.

²⁵ Farwell, O. A. *Notes on the Michigan flora. Rept. Mich. Acad. Sci.* 20:161-195. 1918.

²⁶ Farwell, O. A. *Notes on the Michigan flora. III. Rept. Mich. Acad. Sci.* 22:177-185. 1921.

²⁷ Farwell, O. A. *Contributions to the botany of Michigan, No. 15. Am. Midl. Nat.* 11:72-85. 1928.

has described *P. melleum*, presented several minor additions, and considerably modified his earlier concepts. Gates,²⁸ in 1917, revised the genus for North America, recognizing *P. pubescens*, *P. biflorum*, *P. commutatum*, *P. giganteum* and *P. cobrense*, as well as several varieties. *P. hirtum*, *P. canaliculatum* and *P. parviflorum* were included as doubtful or unidentified species. In 1927, Bush²⁹ accepted twelve North American species.

During the course of the present investigation, the writer has been able to examine many times the amount of herbarium material seen by any previous student of the problem. She has studied in the field all entities herein recognized with the exception of *P. biflorum* and *P. biflorum* var. *hebetifolium*, and at one time or another has had all of the entities except the latter under cultivation. From this abundant material it has been possible to establish the great variation which some of the biological species may exhibit, and to realize that many of the proposed segregates are nothing more than extreme individuals of no taxonomic importance. In the present treatment only four species, two of which are difficult if not impossible to separate completely on morphological grounds, and three varieties of one species are recognized. Only the North American species are discussed in this paper.

MORPHOLOGY

The diagnostic characters separating species in *Polygonatum*, as in many other genera of the Liliaceae, may easily escape notice. They are inconspicuous and often are obscured by extreme variability in size and aspect of the plants.

Underground parts.—The genus is characterized by the presence of creeping knotted branching rhizomes. These have been observed to vary only in size, this variation being correlated with the general size of the whole plant. Deam³⁰ reports that the rhizomes grow near the surface in *P. pubescens* and deep in the ground in *P. biflorum* and *P. commutatum*. This difference appears to be related to differences in habit and habitat.

Stem.—A single upright stem rises from the rhizome each year (or one from each branch of the rhizome). In all North American species the stem is glabrous. It may be terete or ancipital, or sometimes somewhat grooved or channelled, but this character is not definite enough to have much value in species delimitation. The stem is almost strictly vertical to arching to such a degree that the upper part is horizontal. The amount of arching seems due, at least in part, to the size of the plant. The proportion of the leafy to the naked part of the stem seems to be a good character to aid in separating some of the species and varieties. In *P. biflorum* the leafy part is shorter than the lower naked part; in *P. biflorum* var. *melleum* the leafy and naked parts are about equal in length; in *P. biflorum*

²⁸ Gates, R. R. A revision of the genus *Polygonatum* in North America. Bull. Torr. Bot. Club 44:117-126, pl. 4-6. 1917.

²⁹ Bush, B. F. The species of *Polygonatum*. Am. Midl. Nat. 10:385-400. 1927.

³⁰ Deam, Charles C. Flora of Indiana, pp. 319, 320. 1940.

var. *necopinum* and *P. commutatum* the leafy part is usually considerably longer than the naked part.

Leaves.—Some of the best diagnostic characters are to be found in the leaves, both in their shape and in the texture and surface characters. In all the North American species the leaves are alternate. They are broadly oval, elliptic, ovate-lanceolate or nearly linear, the size and shape varying considerably within each of the species. In most cases the leaves are about 2 to 4 times as long as broad, but in *P. biflorum* var. *hebetifolium* they are very long and narrow, being 5 to 9 times as long as broad. In *P. pubescens* and *P. cobrense* the leaves are shortly petiolate; in *P. biflorum* var. *melleum* they vary from sessile to shortly petiolate; in the others they are sessile. The nervation of the leaves presents a nearly constant character which can quite easily be used in the separation of entities. The leaves of *P. pubescens*, *P. biflorum* and vars. *hebetifolium* and *necopinum*, and *P. cobrense* have few major nerves, only the midrib being prominent for the full length of the leaf. The leaves of *P. biflorum* var. *melleum* and *P. commutatum* are many-nerved. In *P. biflorum* var. *melleum* the nerves are all nearly equal in size, prominent in the lower half of the leaf and gradually fading out above the middle of the leaf. In *P. commutatum* the many strong nerves are prominent the full length of the leaf, with the midrib somewhat larger than the rest. *P. pubescens* is easily separated from the other species by the pubescence on the lower surface of the leaves. The hairs are whitish, short, straight and regular. They are found on the minor longitudinal nerves, less frequently on the more prominent nerves. All other species have completely glabrous leaves.

The lowest leaf is a cauline bract, usually set on the stem at a sharper angle than the other leaves. In *P. pubescens* and *P. cobrense* this bract is papery and caducous. In *P. biflorum* and its varieties and in *P. commutatum* it is leaf-like, green and persistent.

Inflorescence.—In most of the species each axillary peduncle bears 1 or 2, or rarely 3, flowers. In *P. biflorum* var. *melleum* the number varies from 2 to 4. In *P. commutatum* there is great variation in the inflorescence, both in the number of flowers (1 to 15) and in the relative lengths of pedicels and peduncle; also the pedicels in one inflorescence are sometimes equal and sometimes very unequal. In *P. biflorum* var. *hebetifolium* the peduncles are very long and slender. Those in *P. pubescens* and *P. cobrense* are strongly and sharply deflexed.

Differences in the position of the lowest peduncle in *P. pubescens*, *P. biflorum* and *P. commutatum*, as pointed out by Deam in his 'Flora of Indiana', have been emphasized by Fernald,³¹ who reports that of the specimens examined by him the lowest peduncle was from the second axil in 66 per cent of the plants of *P. pubescens*, from the third axil in 59 per cent of those of *P. biflorum*, and from the fourth or fifth axil in 72 per cent of those of *P. commutatum*. These figures,

³¹ Fernald, M. L. Specific distinctions between *Polygonatum biflorum* and *P. canaliculatum*. *Rhodora* 46:9-12. 1944.

however, lose some of their significance when it is remembered that the first green "leaf" in *P. biflorum* and *P. commutatum* is actually a cauline bract, and that there is possibility for considerable error in separating these two species on morphological criteria alone.

Perianth.—The size and color of the perianth are of some value in distinguishing species. *P. pubescens* has the smallest flowers, usually 10 or 11 mm. long. The flowers of *P. biflorum* var. *melleum* are also quite small, 12 to 15 mm. long. The other species and varieties have larger flowers, up to 23 mm. long in *P. cobrense*, *P. biflorum* var. *hebetifolium* and *P. commutatum*. In *P. biflorum* var. *hebetifolium* and *P. cobrense* the flowers are larger in proportion to the size of the whole plant than in any other North American species. The flowers are yellowish green in *P. pubescens*, whitish in *P. biflorum* and var. *necopinum*, yellowish in *P. biflorum* var. *melleum* and *P. biflorum* var. *hebetifolium*, and greenish white tipped with darker green in *P. commutatum*. Flower shape may be a good distinguishing character for living plants, but it cannot always be used with entire success on herbarium material. The flowers of *P. pubescens* are broadest below the middle of the perianth tube; the tube is contracted at the base of the perianth lobes, and the lobes are somewhat spreading. The flowers of the other species are nearly cylindric, being broadest at about the middle of the tube; the tube is not contracted at the base of the lobes, and the lobes are scarcely spreading.

Stamens.—The six stamens are inserted on the perianth tube, near the top of the tube in *P. pubescens*, at about the middle in the other species. The filaments of all species may be more or less papillose; they are densely so in *P. pubescens* and sometimes in *P. biflorum* var. *melleum*. In *P. biflorum* and its other varieties and in *P. cobrense* they are usually only slightly papillose. Those of *P. commutatum* vary from densely papillose to entirely smooth. The anthers are introrse.

Pistil.—The ovary is sessile to subsessile, oblong to globose, trilocular, with ovules several to a cell. The style is filiform, shorter than the perianth. The stigma is obtuse or capitate, and obscurely 3-lobed.

Fruit and seeds.—The fruit is a dark blue or black, globose, pulpy, several-seeded berry. The berries are usually larger and have more seeds in the larger *P. commutatum* than in the smaller plants of other species. The seeds are globose to more or less compressed, smooth, pale to brownish, with a stony endosperm.

CYTOLOGY

At the time the present study was undertaken very little was known of the cytology of the American species of *Polygonatum*. Incidental to other studies Cardiff³² had reported a haploid chromosome number of 7 or 8 in material identified as *Salomonina biflora*. His figure of a meiotic metaphase in this species shows 7 bivalents. In 1933, Cartledge³³ reported a haploid number of 10 in *P. biflorum*

³² Cardiff, Ira D. A study of synapsis and reduction. Bull. Torr. Bot. Club 33:271-303, pl. 12-15. 1906.

³³ Cartledge, J. L. Chromosomes of *Polygonatum*. Proc. Pennsylvania Acad. Sci. 7:78, 79. 1933.

and *P. commutatum*. Because of inaccuracies in the existing manuals of the region, it is likely that the former report should be referred to *P. pubescens* and the latter to *P. biflorum*. Chromosome studies on most of the species and varieties recognized in the present treatment were made by the writer independently of and several years in advance of the appearance of Eigsti's comprehensive cytological survey of the eastern North American species.³⁴ Eigsti reported chromosome counts on 19 collections of *Polygonatum* including *P. pubescens*, *P. biflorum*

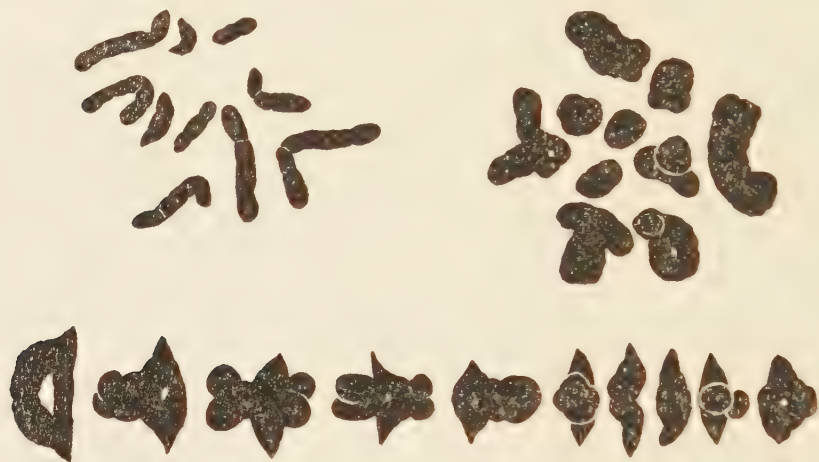


Fig. 1. Chromosomes of *Polygonatum cobrense*. Drawn from Ownbey & Ownbey 1643, from Canyon of Sapillo Creek, Gila National Forest, Grant Co., New Mexico. Upper Left: Metaphase of first pollen grain mitosis, $n = 10$. Upper Right: First meiotic metaphase in pollen mother cell, showing ten bivalents in polar view. Below: Individual bivalents from a single cell, drawn separately in side view. Magnification X 1800.

and *P. commutatum* (the last reported as *P. canaliculatum*). His counts and localities are listed in table 1 along with the writer's counts on these same and other species and varieties from eleven additional localities. Eigsti's counts were determined from colchicine-treated pollen tube mitoses. His technique appears to give a much better preparation than the aceto-carmin smear technique used by the writer to study the chromosomes at meiosis and pollen grain mitosis. This is particularly true in tetraploid material where it was not always possible for her to be sure that the chromosome number is exactly twenty.

From the table it is evident that the haploid chromosome number in all North American species of *Polygonatum* studied in recent years is either 10 or 20. *P. pubescens*, *P. cobrense* and *P. biflorum* with varieties *melleum* and *necopinum* are diploid, $n = 10$. All tetraploid ($n = 20$) specimens studied thus far belong to *P. commutatum*.

Meiosis is regular in all diploid species studied, with the formation of 10 bivalents on the metaphase plate. In the tetraploid *P. commutatum*, however,

³⁴ Eigsti, O. J. A cytological investigation of *Polygonatum* using the colchicine-pollen tube technique. Am. Journ. Bot. 29:626-636. 1942.

TABLE I
SUMMARY OF RECENT CHROMOSOME COUNTS ON THE NORTH AMERICAN
SPECIES OF POLYGONATUM

| Species | Locality | Collector | Chromosome Number | Investigator and Date |
|---|----------------------------|-------------------------------|-------------------|-----------------------------|
| <i>P. pubescens</i> | Strafford Co., N. H. | A. R. Hodgdon | n=10 | Eigsti '40 |
| <i>P. pubescens</i> * | Tolland Co., Conn. | G. S. Torrey | n=10 | Eigsti '41 |
| <i>P. pubescens</i> | Franklin Co., Ohio | Clyde Jones | n=10 | Eigsti '41 |
| <i>P. pubescens</i> | Davidson Co., Tenn. | A. J. Sharp | n=10 | Eigsti '41 |
| <i>P. pubescens</i> | Washtenaw Co., Mich. | J. T. Baldwin, Jr. | n=10 | Eigsti '40, '41 |
| <i>P. pubescens</i> | Baraga Co., Mich. | Edgar Anderson | n=10 | R. Ownbey '39 |
| <i>P. pubescens</i> | Oneida Co., Wisc. | Ruth E. Peck | n=10 | R. Peck '37 |
| <i>P. pubescens</i> | Wabasha Co., Minn. | C. O. Rosendahl | n=10 | Eigsti '41 |
| <i>P. cobrense</i> | Grant Co., N. Mex. | M. Ownbey &
R. Ownbey | n=10 | Ownbey & Ownbey
'42, '44 |
| <i>P. biflorum</i> | Middlesex Co., N. J. | M. A. Chrysler | n=10 | Eigsti '41 |
| <i>P. biflorum</i> | Prince Georges Co.,
Md. | Ronald Bamford | n=10 | Eigsti '41 |
| <i>P. biflorum</i> | Leon Co., Fla. | H. Kurz | n=10 | R. Ownbey '38, '39 |
| <i>P. biflorum</i>
var. <i>melleum</i> | St. Clair Co., Mich. | Edgar Anderson
& R. Peck | n=10 | R. Ownbey '38 |
| <i>P. biflorum</i>
var. <i>necopinum</i> | Pennington Co.,
S. Dak. | M. Ownbey &
R. Ownbey | n=10 | R. Ownbey '39 |
| <i>P. commutatum</i> † | Floyd Co., Va. | J. T. Baldwin, Jr. | n=20 | Eigsti '39, '40, '41 |
| <i>P. commutatum</i> | Wythe Co., Va. | Edgar Anderson
& Wm. Brown | n=20 | R. Ownbey '39 |
| <i>P. commutatum</i> † | Durham Co., N. C. | L. E. Anderson | n=20 | Eigsti '40 |
| <i>P. commutatum</i> † | Washtenaw Co., Mich. | J. T. Baldwin, Jr. | n=20 | Eigsti '41 |
| <i>P. commutatum</i> † | Elkhart Co., Ind. | O. J. Eigsti | n=20 | Eigsti '41 |
| <i>P. commutatum</i> † | Hennepin Co., Minn. | C. O. Rosendahl | n=20 | Eigsti '41 |
| <i>P. commutatum</i> † | Hennepin Co., Minn. | C. O. Rosendahl | n=20 | Eigsti '41 |
| <i>P. commutatum</i> † | Johnson Co., Iowa | W. A. Anderson | n=20 | Eigsti '41 |
| <i>P. commutatum</i> † | Monona Co., Iowa | George Goodman | n=20 | Eigsti '41 |
| <i>P. commutatum</i> | St. Louis Co., Mo. | Maude Lodewyks
& R. Peck | n=20± | R. Peck '36 |
| <i>P. commutatum</i> | St. Louis Co., Mo. | M. Ownbey | n=20± | R. Ownbey '38 |
| <i>P. commutatum</i> † | Cole Co., Mo. | Mrs. H. H. Leake | n=20 | Eigsti '41 |
| <i>P. commutatum</i> | Butler Co., Mo. | Edgar Anderson | n=20± | R. Ownbey '38 |
| <i>P. commutatum</i> | Caddo Parish, La. | Mrs. James L. Dorman | n=20± | R. Ownbey '39 |
| <i>P. commutatum</i> | Cleveland Co., Okla. | O. J. Eigsti | n=20 | Eigsti '39, '40, '41 |
| <i>P. commutatum</i> † | Cleveland Co., Okla. | O. J. Eigsti | n=20 | Eigsti '40, '41 |

*Described as pubescent, and diploid, but listed as *P. canaliculatum*—obviously a mistake.

†Reported as *P. canaliculatum*, a name now considered to be synonymous with *P. biflorum* and unavailable, therefore, for the tetraploid species.

there appears to be always some multivalent formation. This may result in unequal distribution of the chromosomes to the daughter nuclei, possibly accounting for seeming variation from the expected 20 chromosomes at mitosis in the pollen grains. Such irregularities are much more likely to be evident at this division than later at the pollen tube mitosis studied by Eigsti.

No karyotypic differences between the species other than tetraploidy are reported by Eigsti. In all of the diploid species studied there are 6 long and 4 short chromosomes; 12 long and 8 short, in the tetraploid. Eigsti states that in the diploid species 6 chromosomes have sub-terminal and 4 have sub-median insertions; in the tetraploid, 12 chromosomes have sub-terminal, 8 have sub-median insertions. An examination of his photographs, however, reveals that in one-third of his collections of *P. pubescens* and in all of his collections of *P. biflorum* there are 5 chromosomes with sub-median and 5 with sub-terminal constrictions. This latter condition agrees with the writer's observations in *P. biflorum* var. *melleum* and *P. biflorum* var. *necopinum*. The chromosomes of *P. cobrense* are shown in fig. 1.

Stomata size and distribution have recently been suggested and found useful in certain groups of plants as a means of detecting polyploidy through the use of herbarium specimens.^{35, 36, 37} Sax and Sax found, in the genera which they investigated, that stomata frequency was a better index to polyploidy than stomata length. Babcock and Stebbins use stomata length. In *Polygonatum* also, stomata length is of more value. The chromosome numbers of the diploid *P. biflorum* and the tetraploid *P. commutatum* are correlated with either stomata measurement. In general, the stomata of *P. biflorum* are shorter and more frequent than those of *P. commutatum*, but there is considerable overlapping in the size and distribution ranges. In the diploid *P. pubescens*, the size of the stomata is similar to that in *P. biflorum*, but the frequency is like that in *P. commutatum*. The diploid *P. biflorum* var. *melleum* has very short stomata. On the other hand, *P. cobrense*, also diploid, and *P. biflorum* var. *hebetifolium*, whose chromosome number is unknown but whose morphology suggests that it is diploid, have stomata as long as the longest found in the tetraploid. Thus it is apparent that, although stomata size is of some use in separating the closely related diploid *P. biflorum* and tetraploid *P. commutatum*, it cannot be relied upon, in the genus as a whole, as a method of detecting polyploids.

In the species investigated, a much stronger correlation was found between stomata size and flower length than between stomata size and chromosome number. The flowers of *P. biflorum*, like the stomata, are usually but not always shorter than those of *P. commutatum*. *P. pubescens* and *P. biflorum* var. *melleum* have short flowers and stomata; *P. cobrense* and *P. biflorum* var. *hebetifolium* have very long flowers and stomata.

³⁵ Sax, K., and H. J. Sax. Stomata size and distribution in diploid and polyploid plants. Journ. Arnold Arboretum 18:164-172, pl. 205. 1937.

³⁶ Babcock, E. B., and G. L. Stebbins, Jr. The American species of *Crepis*, their interrelationships and distribution as affected by polyploidy and apomixis. Carnegie Inst. Wash. Publ. No. 504. 1938.

³⁷ Stebbins, G. L., Jr. Notes on some systematic relationships in the genus *Paeonia*. Univ. California Publ. Bot. 19:245-266. 1939.

DISTRIBUTION

Polygonatum is widely distributed in north temperate regions. There are many more species in Europe and in temperate Asia than in North America, but these have not been studied in this investigation. In North America, the genus is found from the Atlantic Ocean to the Black Hills of South Dakota, and from southern Canada to northeastern Mexico. One species, *P. cobrense*, occurs in a restricted area in southwestern New Mexico and eastern Arizona.

GENERIC RELATIONSHIP

The two genera perhaps most closely related to *Polygonatum* are *Streptopus* and *Disporum*, both with extensive north temperate ranges. Baker³⁸ included *Polygonatum* with *Convallaria* and other genera in the tribe Convallarieae of the Asparagaceae. What is perhaps a better way to treat the genus is that found in Bentham and Hooker's 'Genera Plantarum',³⁹ where it is included with *Streptopus*, *Disporum*, *Smilacina*, *Maianthemum*, etc., in the tribe Polygonateae of the Liliaceae, and in Engler and Prantl's 'Natürlichen Pflanzenfamilien',⁴⁰ where it is placed with *Clintonia*, *Tovaria* [*Smilacina*], *Maianthemum*, *Disporum*, *Streptopus*, etc., in the Asparagoideae-Polygonateae of the Liliaceae.

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ABBREVIATIONS

The herbaria from which loans of material for study have been obtained and from which citations are made in this treatment are indicated by the following abbreviations:

C—Herbarium of the National Museum of Canada.

D—Personal Herbarium of Charles C. Deam.

Farwell—Personal Herbarium of O. A. Farwell.

FM—Herbarium of the Chicago Museum of Natural History (Field Museum).

G—Gray Herbarium of Harvard University.

³⁸ Baker, J. G. Revision of the genera and species of Asparagaceae. Journ. Linn. Soc. [Lond.] Bot. 14:508-632, pl. 17-20. 1875.

³⁹ Bentham, G., and J. D. Hooker. Genera Plantarum 32:768, 769. 1883.

⁴⁰ Krause, K., in Engler & Prantl, Die natürlichen Pflanzenfamilien, 2. Aufl. 15a:368-370. 1930.

- M—Herbarium of the Missouri Botanical Garden.
 Minn—Herbarium of the University of Minnesota.
 MS—Herbarium of the Michigan State College of Agriculture.
 NY—Herbarium of the New York Botanical Garden.
 NYCP—Herbarium of the New York College of Pharmacy.
 RM—Rocky Mountain Herbarium of the University of Wyoming.
 UF—Herbarium of the Agricultural Experiment Station, University of Florida.
 UM—Herbarium of the University of Michigan.
 US—United States National Herbarium.
 WS—Herbarium of the State College of Washington.
 WVU—Herbarium of West Virginia University.

TAXONOMY

Polygonatum [Tourn.] Miller, Gard. Dict. Abridg., ed. 4. 1754, in part; Adans., Fam. 2:54. 1763; All., Fl. Ped. 1:130. 1785, in major part; Baker in Journ. Linn. Soc. [Lond.] Bot. 14:552-561. 1875; Benth. & Hook., Gen. Pl. 3^d:768, 769. 1883; Krause in Engler & Prantl, Nat. Pflanzenf. 2. Aufl. 15a:368-370. 1930.

- Convallaria* L., Gen. Pl., ed. 5, p. 148. 1754, in part.
Salomonina Heist. ex Fabricius, Enum. Pl. Hort. Helmstad., ed. 2, p. 38. 1763.
Evallaria Neck., Elem. 3:189. 1790.
Axillaria Rafin. in Journ. Phys. 89:261. 1819.
Siphyalis Rafin., Fl. Tellur. 4:17. 1836.
Campydorum Salisb., Gen. Pl. Fragm., p. 64. 1866.
Sigillum [Trag. ex] Montand., Guide Bot., p. 310. 1868.
Periballanthus Franch. & Sav., Enum. Pl. Jap. 2:524. 1879.

Perennial herbs with horizontal, creeping, knotted rhizomes and fibrous roots; stem erect or arching, unbranched, glabrous or pubescent (glabrous in all North American species), naked below, leafy above, with one or more papery sheathing bracts at the base; leaves alternate, opposite or verticillate (alternate in all North American species), amplexicaul, sessile, or shortly petiolate, broadly oval to ovate-lanceolate to linear, glabrous on both sides or with a fine pubescence on the veins below; inflorescence axillary, the solitary peduncles each bearing a single flower, or two or more jointed pedicels each bearing a flower; peduncles and pedicels glabrous or pubescent (glabrous in all North American species); floral bracts much reduced, subulate, caducous; flowers pendulous, with the calyx and corolla united into a cylindric tube, 6-lobed at the top; perianth lobes usually shorter than the tube, sometimes spreading in the mature flower, glandulose-barbate at the tip inside; stamens six, included, inserted on the perianth tube; filaments filiform or flattened, smooth to roughly papillose; anthers oblong-linear to sagittate, 2-lobed at the base, introrse; ovary sessile to subsessile, oblong to globose, 3-locular; style filiform, shorter than the perianth; stigma obtuse or capitate, obscurely 3-lobed; ovules several in a cell; fruit a dark blue or black, globose, pulpy, several-seeded berry; seeds globose to more or less compressed, smooth, pale to brownish, with stony endosperm.

TYPE SPECIES: *Convallaria Polygonatum* L., Sp. Pl. 1:315. 1753 (= *Polygonatum officinale* All., Fl. Ped. 1:131. 1785).

KEY TO THE SPECIES AND VARIETIES

- a. Cauline bract papery, caducous; peduncles strongly and sharply deflexed.
- b. Leaves pubescent on the veins beneath; flowers small, 8 to 14 (usually 10 or 11) mm. long; perianth tube constricted at base of lobes, lobes spreading at anthesis; filaments inserted near the top of the tube; diploid ($n = 10$). 1. *P. pubescens*
- bb. Leaves glabrous on both sides; flowers large, 17 to 23 mm. long; perianth tube cylindrical, not constricted, lobes erect at anthesis; filaments inserted near the middle of the tube; diploid ($n = 10$) 2. *P. cobrense*
- aa. Cauline bract green, leaf-like, persistent; peduncles arcuate, not strongly deflexed; plant entirely glabrous; flowers usually 12 to 23 mm. long; perianth tube cylindrical, not constricted, lobes scarcely spreading; filaments inserted near the middle of the tube.
- c. Chromosome complement diploid ($n = 10$);* plants dainty, usually less than 6 dm. high; peduncles 1- or 2 (to 4)-flowered; leaves with only the mid-vein prominent for the full length.
- d. Upper leafy portion of the stem usually shorter than lower naked portion; leaves elliptic-lanceolate, few-nerved; peduncles 1- or 2-flowered; flowers 11 to 19 (usually 13 to 15) mm. long; widespread in eastern United States. 3. *P. biflorum*
- dd. Upper leafy portion of the stem about equalling lower naked portion in length; leaves variable in shape, elliptic-lanceolate to broadly elliptic, many-nerved; peduncles 2- to 4-flowered; flowers 12 to 15 mm. long; Michigan and Ontario, in the vicinity of Lake St. Clair. 3a. *P. biflorum* var. *melleum*
- ddd. Upper leafy portion of the stem about equalling lower naked portion in length; leaves oblong-lanceolate, 5 to 9 times as long as broad, few-nerved; peduncles 1- or 2-flowered; flowers large, 20 to 23 mm. long; along the Apalachicola River, western Florida. 3b. *P. biflorum* var. *hebetifolium*
- dddd. Upper leafy portion of the stem longer than lower naked portion; leaves elliptic-lanceolate, few-nerved; peduncles 2-flowered; flowers 15 to 17 mm. long; Black Hills of South Dakota. 3c. *P. biflorum* var. *necopinum*
- cc. Chromosome complement tetraploid ($n = 20$); plants generally coarser, more robust, usually more than 6 dm. high, often much larger; peduncles 1- to 15 (usually 3 or more)-flowered; leaves with numerous veins prominent the full length; upper leafy portion of the stem usually longer than the lower naked portion. 4. *P. commutatum*

* Chromosome number given at the beginning of the paragraph here because it is the best character separating *P. biflorum* and *P. commutatum*; in other places it is supplementary information.

1. *Polygonatum pubescens* (Willdenow) Pursh, Fl. Am. Sept. 1:234. 1814.

Convallaria pubescens Willdenow, Hort. Berol. 1:45, pl. 45. 1806.⁴¹

Polygonatum multiflorum β. *pubescens* Wood, Class-book of Bot., ed. 1, p. 396. 1845.

Polygonatum multiflorum β. *americanum* Hooker, Fl. Bor. Am. 2:176. 1839 (apparently typical part).

Polygonatum biflorum sensu A. Gray, Manual, ed. 2, p. 466. 1856, and subsequent editions, not *P. biflorum* (Walter) Elliott, Sketch Bot. S. C. & Ga. 1:393. 1817.

Polygonatum multiflorum δ. *latifolium* Wood, Class-book of Bot. Fl. U. S. & Can., p. 714. 1861.

Polygonatum biflorum γ. *latifolium* Wood, Am. Bot. & Flor., p. 346. 1870.

Polygonatum cuneatum Greene, Leaflets 1:181. 1906.

Polygonatum pubescens var. *cuneatum* Farwell in Bull. Torr. Bot. Club 42:253, pl. 13, B. 1915; Am. Midl. Nat. 11:77. 1928.

⁴¹ Synonyms are cited chronologically according to type.

Polygonatum pubescens f. *cuneatum* Victorin in Contrib. Lab. Bot. Univ. Montreal 14:28. 1929.

Polygonatum boreale Greene, Leaflets 1:181. 1906.

Polygonatum pubescens var. *boreale* Farwell in Am. Midl. Nat. 11:76. 1928.

Polygonatum boreale var. *australe* Farwell in Bull. Torr. Bot. Club 42:254, pl. 14, B. 1915.

Polygonatum pubescens australe Gates in Bull. Torr. Bot. Club 44:119, pl. 4, A. 1917.

Polygonatum pubescens var. *boreale* subvar. *australe* Farwell in Am. Midl. Nat. 11:77. 1928.

Polygonatum boreale var. *multiflorum* Farwell in Rept. Mich. Acad. Sci. 20:170. 1918.

Polygonatum Farwellii Bush in Am. Midl. Nat. 10:390. 1927.

Polygonatum pubescens var. *multiflorum* Farwell in Am. Midl. Nat. 11:77. 1928.

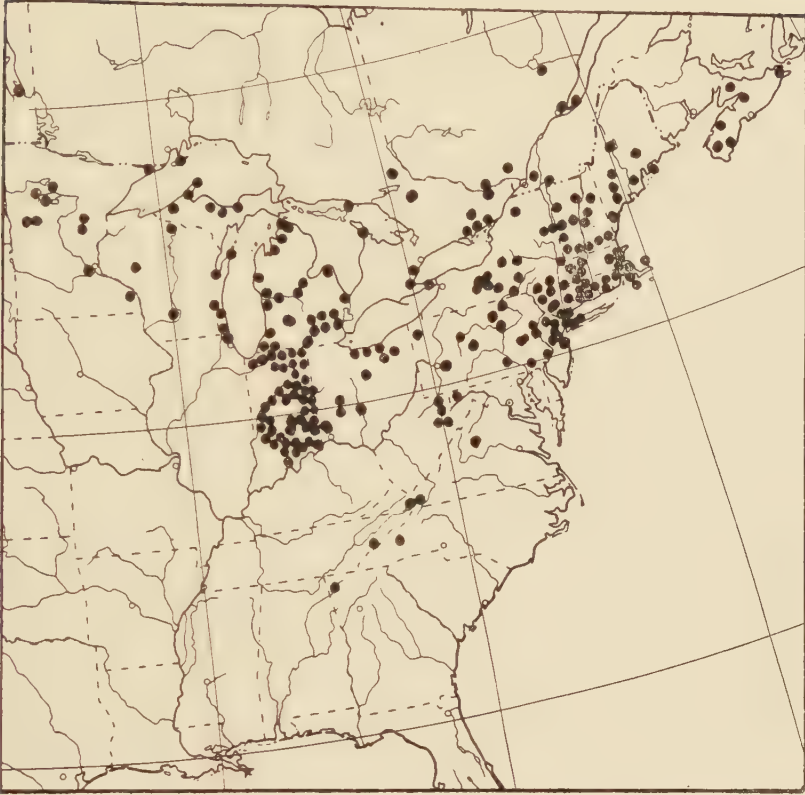
Polygonatum pubescens f. *fultius* Fernald & Harris in Rhodora 35:404, fig. 1. 1933.

Perennial herb, usually 3 to 6, but occasionally as much as 9 dm. high; rhizome slender; stem slender, erect or slightly arched at top, upper leafy portion of stem shorter than lower naked portion; leaves alternate, frequently secund, elliptic-lanceolate to elliptic or broadly oval, narrowed at the base to a short petiole, blade rounded to cuneate at the base, narrowed abruptly to an obtuse apex, 3.5 to 15 cm. long, 1 to 7 cm. broad, glabrous above, glaucous, often minutely papillose, and with a fine pubescence on the minor nerves beneath, prominent nerves 3 to 9; cauline bract subulate, papery, caducous; peduncles axillary, solitary, slender, glabrous, strongly and sharply deflexed, usually none from the axil of the lowest leaf, usually 1- or 2 (occasionally 3 to 5)-flowered; pedicels slender, glabrous, subequal, usually shorter than the peduncle; flowers yellowish green, smaller than in the other North American species; perianth 8 to 14 (usually 10 or 11) mm. long, 2.5 to 5 mm. broad in pressed material, contracted at the base of the perianth lobes, minutely papillose inside; lobes of the perianth spreading at anthesis, papillose inside; filaments densely papillose, inserted near the top of the perianth tube; berry dark blue, usually between 7 and 10 mm. in diameter.

This species is easily distinguished by its pubescent leaves, deflexed peduncles and small flowers, with the perianth tube contracted at the base of the spreading lobes and the stamens inserted near the top of the tube. The numerous varieties which have been proposed were based mostly on leaf shape and size alone, and appear to be mere phases of a continuous series. None appears to have a significant geographical distribution. The larger, more vigorous-looking plants may have peduncles with from 3 to 5 flowers.

DISTRIBUTION: In usually moist, rich woods, Nova Scotia and New England, south along the Appalachian Mountains to northern Georgia, west to Indiana, Illinois, Wisconsin, Minnesota, and Manitoba (Map 1).

NOVA SCOTIA. GUYSBOROUGH CO.: Boylston, June, 1890, *Hamilton* (C). COLCHESTER CO.: wooded banks, Truro, June 11, 1883, *Macoun* (C). CUMBERLAND CO.: dryish woods along Kennedy Brook, Springhill Junction, July 18, 1920, *Pease & Long* 20756 (G). LUNENBURG CO.: Bridgewater, July 21, 1910, *Macoun* (C, FM). ANNAPOLIS CO.: mixed woods, south slope of North Mt., n. of Middleton, July 21, 1920, *Long* 20757 (C,



Map 1. Distribution of *Polygonatum pubescens*. Since the map was made, additional specimens from New Jersey, West Virginia and Ohio have been seen. Based on Goode Base Map No. 102. By permission of The University of Chicago Press.

G). DIGBY CO.: moist thickets and borders of woods, Hectanooga, July 31, 1920, *Long & Linder 20758* (G).

QUEBEC. LAKE ST. JOHN CO.: on boulders, margins of woods, vicinity of St. Jerome, Laurentide Mts., June 30, 1920, *Victorin 10016* (G). MONTMORENCY CO.: exposed rocks, Grosse Isle, 40 mi. below Quebec, Aug. 28, 1922, *Victorin 16004* (G, US). QUEBEC CO.: Montmorency Falls, June 28, 1905, *Macoun* (C). MISSISQUOI CO.: dry limestone ledge, Philipsburg, Aug. 10, 11, 1923, *Knowlton* (G); woods, limestone, Philipsburg, May 24, 1930, *Victorin & Germain 34161* (G). CHAMBLY (?) CO.: Montagne de Beloeil, June 1, 1920, *Victorin 11005* (G). TERREBONNE CO.: woods, Lac Tremelant, July 31, 1922, *Churchill* (G). HULL CO.: rich woods, Hull, May 27, June 10, 1905, *Harrington 2285* (C); Hull cemetery, June 3, 1911, *Macoun* (C).

ONTARIO. CARLETON CO.: woods, Ottawa, May 28, 1893, *Macoun* (C); Ottawa, Aug. 20, 1894, *Macoun* (G); woods, McKays Bush, Ottawa, Aug. 21, 1894, *Macoun* (C); Dows swamp, by Rideau River, above Billings Bridge, May 21, 1903, *Macoun* (C). LEEDS CO.: Jones Falls, May 26, 1891, *Fowler* (US). FRONTENAC CO.: Battersea, June 1, 1893, *Fowler* (M, MS); Sharbot Lake, July 16, 1898, *Fowler* (FM). HASTINGS CO.: rich woods, vicinity of Belleville, May 30, 1877, *Macoun* (C). PEEL CO.: woods, Snelgrove, June 3, 1898, *White* (C). WENTWORTH CO.: woods, West End Spring, Hamilton, 1892, *Dickson* (C). WELLAND CO.: Point Abino, Lake Erie, Aug. 28, 1896, *A.A.A.S.*

Excursion (NY). NIPissing DIST.: Skunk Lake Portage, Timagami Provincial Forest, Aug. 25, 1932, *Krotkov* 5231 (G); rich woods, Cache Lake, Algonquin Park, June 12, 1900, *Macoun* (C). MANITOULIN DIST.: crevices and talus of hornblend cliffs and ledges, Cloche Peninsula, June 29, 1934, *Fernald & Pease* 3239 (G). BRUCE CO.: maple grove, Lake Ira, Bruce Peninsula, June 4, 1934, *Krotkov* 8854 (G).

MANITOBA. DISTRICT NOT DETERMINED: Lake Winnipeg Valley, 1851, *Bourgeau* (G).

MAINE. PENOBSCOT CO.: Orono, June, 1895, *Keinstead* 1020 (US). HANCOCK CO.: trail between Jordans Pond and Eagle Lake, Mt. Desert, June 28, 1889, *Redfield* 16438 (M). KNOX CO.: Union, 1916, *Cole* 271 (US); rich shaded woods, near Washington Pond, 3 mi. n. of Washington, Aug. 24, 1929, *Steyermark* 881 (M). SOMERSET CO.: Kineo, Sept. 13, 1893, *Kennedy* (G). FRANKLIN CO.: damp woodland, South Chester-ville, May 18, 1902, *Eaton* (G). OXFORD CO.: Hartford, May, 1885, *Parlin* (G); dry wooded banks, Buckfield, Aug., 1895, *Parlin* (Minn). CUMBERLAND CO.: North Gray, July 10, 1915, *Fellows* 7109 (US). YORK CO.: thin woods, South Berwick, May 27, 1934, *Neal* 97 (Minn).

NEW HAMPSHIRE. COOS CO.: Randolph, Sept. 2, 1903, *Moore* 1465 (G). GRAFTON CO.: rich woods, Hanover, May, 1936, *Beetle* 240 (WS), 1098 (RM); alluvial woods, North Woodstock, July 15, 1915, *Fernald* 11647 (G); Hanover, May 25, 1883, *Hitchcock* (M, Minn). ROCKINGHAM CO.: wooded bank of pond, Derry, Aug. 25, 1917, *Batchelder* (NY). HILLSBORO CO.: rich damp woods, Wilton, May 16, 1929, *Beattie* (RM); wooded roadside, Mason, May 28, 1914, *Batchelder* (US); wooded roadside bank, Merrimack, June 2, 1920, *Batchelder* (M); wooded roadside, Peterborough, Sept. 13, 1927, *Batchelder* (M). CHESHIRE CO.: woods, Jaffrey, July, 1897, *Robinson* 202 (G).

VERMONT. CALEDONIA CO.: Peacham, May 22, 1887, *Blanchard* (FM, M, NY, RM, US). ORANGE CO.: palisades, Fairlee, July 6, 1927, *Mathias* 140 (M, NY). CHITTENDEN CO.: Charlotte, May 26, 1878, *Horsford* (FM); rich moist woods, Milton, May 22, 1936, *Knowlton* (D). ADDISON CO.: rich woods, Bristol, July 11, 1935, *Knowlton* (D). RUTLAND CO.: woods, edge of Scanlon swamp, Brandon, May 16, 1921, *Dutton* (FM, M). BENNINGTON CO.: East Dorset, July, 1867, *Ames* (UM); Manchester, July 7, 1898, *Day* 173 (FM, G, US). WINDHAM CO.: Westminster, Aug. 26, 1848, *Holton* (FM); at edge of woods on top of moist cliff, Wardsboro, May 26, 1937, *Moldenke & Moldenke* 9503 (NY); woods, Westminster, June 16, 1898, *Robinson* 47 (G).

MASSACHUSETTS. ESSEX CO.: moist woods, Essex Lakes, Hamilton, May 26, 1870, *Morong* (NY); Beverly, Sept., 1892, *ex herb. Peabody* (G); Marblehead, June 5, 1900, *Piper* (WS). MIDDLESEX CO.: woods, Horn Pond Mt., Woburn, May 14, 1905, *Bartlett* 70 (UM); Westford, *Fletcher* (G); Seavers Woods, near boundary between Newton and Weston, May, 1893, *ex herb. Gilbert* (G); Auburndale, May 23, 27, 1894, *ex herb. Gilbert* (G); fresh pond, Cambridge, *Gray* (G); Stony Brook, May 15, 1897, *Greenman* 2288 (M); rich woods, Shirley, May 30, 1914, *Hunnewell & St. John* 1608 (WS); damp woods, Melrose, May 30, 1876, *Morong* (M); Ashland, June 30, 1877, *ex herb. Morong* (NY); open woods along Estabrook road, vicinity of Concord, May 27, 1915, *Norton* 195 (US); Arlington, May 22, 24, 1900, *Piper* (WS); South Framingham, May 14, 1890, *Sturtevant* (M); vicinity of Cambridge, May 30, 1891, *Underwood* 2760 (NY). SUFFOLK CO.: near Boston, 1816, *Boott* (US); Oak Island, May 23, 1897, *Greenman* 2284 (M); Revere, Aug. 28, 1882, *Perkins* (C). NORFOLK CO.: cleft in rock, Stoughton, May 13, 1909, *Blake* (US); Blue Hills, May 28, 1854, *ex herb. Boott* (G); Brookline, *ex herb. Faxon* (G); Wellesley, May 18, 1889, *ex herb. Harlow* (NY); Blue Hill, near entrance to Blue Hill Reservation, Milton, May 20, 1911, *Kennedy* (G); Milton, May 27, 1900, *Murdoch* 471 (FM). PLYMOUTH CO.: Middleboro, June 20, 1902, *Murdoch* 1134 (FM). BARNSTABLE CO.: Provincetown, May 22, 1907, *Greenman* 3013 (M); Provincetown, Sept. 2-11, 1901, *Hollick* (NY). DUKES CO.: Chappaquiddick Island, Sept. 15, 1917, *Bicknell* (NY); damp woods, near brook, Menemsha, Chilmark, June 10, 1917, *Seymour* 1154 (G, US); low ground, off North Road, Chilmark, June 10, 1917, *Seymour* 1899 (G); woods, West Tisbury, June 8, 1917, *Seymour* 1900 (G). BRISTOL CO.: Nonquit, May 29, 1889, *Sturtevant* (M). FRANKLIN CO.: Sugar Loaf, 1818, *ex herb. Cooley* (MS); Sunderland, May 25, 1880, *Minott* (US); cool rich woods, Monroe Bridge, Mon-

roe, May 15, 1915, *St. John & Hill 11009* (WS); Ashfield, Aug. 8, 1909, *Williams* (G). HAMPSHIRE CO.: Amherst, May, 1890, *Morris* (Minn); roadside banks in wooded country, Huntington, Aug. 17, 1912, *Robinson 485* (G). HAMPDEN CO.: Russell, May 31, 1873, *Rusby* (UM); shaded brookside, Russell, May 17, 1913, *St. John & White 90* (WS). BERKSHIRE CO.: hedgerow, Adams, Aug. 27, 1901, *Day 101* (G); steep rocky wooded slope, North Adams, June 23, 1913, *Fernald & Long 9248* (G).

RHODE ISLAND. PROVIDENCE CO.: Cat Swamp, Providence, May 24, 1900, *Chamberlain 86* (US); woods, Providence, June, 1866, *Thurber* (G); Lonsdale, May 15, 1904, *Williams* (G).

CONNECTICUT. WINDHAM CO.: dry, but rich, woods and thickets, Thompson, May 17, 1918, *Weatherby 4224* (US). NEW LONDON CO.: damp rocky woods, Center Groton, Groton, May 28, 1933, *Jansson* (RM); Greeneville, June 3, 1885, *Lumsden* (C). MIDDLESEX CO.: Middletown, June, 1830, *Buckley* (M). HARTFORD CO.: fence rows, Southington, June 29, 1898, *Andrews 348* (G); hedges and fence rows, Southington, May 30, 1898, *Andrews 349* (G); woods, Southington, May 7, 1897, *Bissell 209-2659* (M); Glastonbury, May 28, 1932, *Denslow* (NY); Wethersfield, June, July, 1875, *Wright* (G); Farmington, June 4, 1884, *Wright* (M). NEW HAVEN CO.: New Haven, May 20, 1884, *Safford 42* (US). LITCHFIELD CO.: wooded trap-rocks, Woodbury, June 14, 1933, *Eames 11546* (G). FAIRFIELD CO.: Fairfield, May 17, 1895, *Eames* (US); edge of rich woods, Fairfield, May 17, 1896, *Eames 1* (G); Easton, May 10, 1905, *Eames & Godfrey 69* (UF); Redding, June 28, 1905, *Godfrey* (UF); vicinity of Greens Farms, July 5, 1894, *Pollard 144* (US).

NEW YORK. WARREN CO.: sandy roadside woods, w. of Odels, w. of Lake Sunnyside, n. of Glens Falls, Aug. 24, 1916, *Burnham* (G). WASHINGTON CO.: gravelly sandy woods, near Tripoli Cemetery, southern West Fort Ann, May 31, 1915, *Burnham* (G); road, Podunk to Wiggins mine, West Fort Ann, June 8, 1917, *Burnham* (G). RENSSELAER CO.: Troy, 1828, 1834, *Hall* (FM). COLUMBIA CO.: near Turedy Lake, May 30, 1926, *Beale & party* (NY); woods, Copake Falls, Aug. 28, 1914, *Britton, Taylor & Stetson* (NY). GREENE CO.: Windham, July 28-31, 1909, *Taylor 864* (NY); Onteora, vicinity of Tannersville, July 2, 20, 1891, *Vail* (NY). DELAWARE CO.: Arkville, May 29-31, 1915, *Mulford & Wilson* (NY). DUTCHESS CO.: rich woods, vicinity of Clove, Sept. 7, 1915, *Standley & Bollman 12389* (US). ULSTER CO.: Panther Mt., Aug. 14, 1919, *Denslow* (NY); Shandaken, Aug. 30, 1919, *Denslow* (NY). SULLIVAN CO.: woods, near Wurtsboro, June, 1873, *Eggert* (M). ORANGE CO.: Southfields, Tuxedo, May 10, 1922, *Denslow* (NY); Otisville, Aug. 30, 1922, *Denslow* (NY); Goshen, Aug. 31, 1922, *Denslow* (NY); woodland, Highland Falls, May 23, 1915, *Pennell 2395* (NY). WESTCHESTER CO.: woods, Bronxdale, May 7, 1902, *Burnham 835* (G); Mount Pleasant, May 15, 1922, *Denslow* (NY); North Castle, May 23, 1923, *Denslow* (NY); vicinity of New Rochelle, 1908, *Garvens* (FM); woodland, North Tarrytown, May 9, 1915, *Pennell 2376* (NY). ROCKLAND CO.: Haverstraw, May 19, 1921, *Denslow* (NY); Ramapo, May 24, 1922, *Denslow* (NY); rocky woodland, Snedens Landing, Nov. 3, 1914, *Pennell 2334* (NY). BRONX CO.: Van Cortlandt Park, Caryl, Yonkers, May 11, 1893, *Bicknell 552* (NY); McLeans Woods, Bronx, May 13, 1913, *Holtzoff* (NY); Van Cortlandt Park, New York City, Apr. 29, 1921, *House 7726* (C); Bronx Park, New York City, May 11, 1896, *Nash 86* (NY). NEW YORK CO.: New York City, May 25, 1893, *ex herb. Curtis* (Minn); 54th St., New York City, May, 1848, *Leggett* (NY). SUFFOLK CO.: hilly rich woods, Cold Spring Harbor, May 23, 1928, *Ferguson 6529* (NY). NASSAU CO.: Roslyn, Sept. 12, 1919, *Ferguson* (NY); hilly rich woods, n. w. of Platsdale, July 17, 1926, *Ferguson 4160* (NY); hilly wet rich woods, Millneck, May 25, 1926, *Ferguson 4807* (NY). QUEENS CO.: Richmond Hill, May 11, 1904, *Bicknell* (NY); North Beach, May 16, 1927, *Ferguson 5410* (NY). ST. LAWRENCE CO.: rich woods, Canton, May 23, 1915, *Phelps 1384* (C, G, NY, US). ONEIDA CO.: ravine sides and rich woods, Utica, May 16, 1902, *Haberer 923* (G). ONONDAGA CO.: swamp, e. of Syracuse, *Bell* (US); near Syracuse, 1891, *Straub* (US). CHENANGO CO.: Bainbridge, Aug. 13, 1932, *Denslow* (NY). BROOME CO.: Binghamton, 1895, *Clute* (NY); rich woods, South Mt., Binghamton, *Millsbaugh 885* (FM). TOMPKINS CO.: leaf-mold on ledges, north side of

Fall Creek Ravine, above Beebe Lake, Ithaca, May 17, 1915, *Eames* 3737 (G, Minn); woods, Fall Creek Ravine and vicinity, north shore of Beebe Lake, Ithaca, May 27, 1915, *Eames* 3744 (FM, G); rich woods, n. w. of Enfield Falls, Enfield, June 11, 1917, *Gersbony* 7884 (G); ravines, Ithaca, May, 1903, *Kauffman* (UM); flats near Lick Brook, Ithaca, May 23, 1920, *Muenschel & Bechtel* 113 (WS); Six-mile Creek, Ithaca, May 26, 1883, *Pearce* (US). YATES CO.: without exact locality, *Sartwell* (FM). ONTARIO CO.: open woods, east side of Hemlock Lake, Canadice, May 18, 1915, *Thomas* 3743 (G); moist woods, Geneva, June 4, 1882, *Wing* (M). LIVINGSTON CO.: glen, west side of Hemlock Lake, Conesus, May 20, 1915, *Thomas* 3738 (G, M). COUNTY NOT DETERMINED: South Meadow, Adirondacks, Sept. 16, 1892, *ex herb. Clarke* (NY); Balsam Lake, Catskills, July, 1886, *Van Brunt* (NY).

NEW JERSEY. SUSSEX CO.: rich woods, Andover Junction, May 30, 1917, *Mackenzie* 7642 (NY); wooded hillside, Sucker Pond, May 29, 1920, *Mackenzie* (NY); Franklin, Aug., 1879, *Rusby* (UM); woods, Hamburg, June 1, 1892, *ex herb. Van Sickle* (US). PASSAIC CO.: Butler, Sept. 22, 1922, May 14, 1923, *Denslow* (NY); woodlands, Greenwood Lake, May 19, 1907, *Mackenzie* 2574 (M). BERGEN CO.: Fort Lee, May, 1898, *Wootton* (US). UNION CO.: Summit, July 30, 1868, *Leggett* (NY). SOMERSET CO.: Chimney Rock, May 21, 1932, *Drushel* 7905 (M); dark moist woods along brook, Watchung, May 10, 1931, *Moldenke* 1512 (NY). MIDDLESEX CO.: woodlands, Metuchen, May 18, 1919, *Mackenzie* (NY). MONMOUTH CO.: thickets, Cream Ridge, May 29, 1922, *Dreisbach* 939 (FM); rich bottom woods, Freehold, Aug., 1917, *Mackenzie* 7926 (NY); shaded marl slopes, Marlboro, Sept., 1917, *Mackenzie* 8088 (NY); wooded marl banks, Marlboro, May 3, 1919, *Mackenzie* (NY). BURLINGTON CO.: wooded terraces along tributary, Rancocas Creek, 1 mi. n. e. of Pemberton, May 15, 1917, *Long* (WVU).

PENNSYLVANIA. BRADFORD CO.: woods, Athens, May 27, 1900, *Barbour* 870 (RM). TIOGA CO.: Blossburg, Sept. 24, 1928, *Eggleston & Kelly* 22766 (M, US). LYCOMING CO.: Deer Hole Mt., South Williamsport to summit, Sept. 21, 1928, *Eggleston & Kelly* 22754 (US). MONROE CO.: Pocono Plateau, July, Aug., 1904, *Harshberger* (FM, G, M, RM, US). NORTHAMPTON CO.: Easton, July 14, 1896, *Tyler* (NY). SCHUYLKILL CO.: Uhls Mill, Spring Mountain, May 2, 12, 1906, *Williamson* (NY). DELAWARE CO.: rocky woods, Rockdale, Sept. 6, 1914, *Pennell* 1658 (NY); rich woods, Wawa, May 3, 1915, *Pennell* 2368 (NY). LANCASTER CO.: Mountville, May, 1889, *Eby* (M); Cedar Hill, 3 mi. n. of Lancaster, Apr. 24, 1889, *Small* (FM). CUMBERLAND CO.: near Eberlys Mill, May 4, 1888, *Small* (FM). CLEARFIELD CO.: dry rich woods, 2 mi. n. w. of Du Bois, May 18, 1941, *Wahl* 947 (WS). BLAIR CO.: Bellwood, May 18, 1904, *Jennings* (M photo). WESTMORELAND CO.: woodlands, hillside, Chestnut Ridge, May 19, 1935, *Bright* 12426 (Minn); ravine, North Trafford, May 29, 1937, *Emig* (M). CRAWFORD CO.: Hartstown, May 31, 1937, *Emig* (M); edge of woods, Hemlock Island, 5 mi. w. s. w. of Linesville, May 19, 1932, *Graham* (NY).

DELAWARE. COUNTY NOT DETERMINED: woodlands, June, 1865, *Canby* (NYCP).

MARYLAND. GARRETT CO.: without locality, July 24, 1878, *Smith* (US).

WEST VIRGINIA. BROOKE CO.: Franklin Community, Wellsburg, June 6, 1937, *Emig* (M). OHIO CO.: shaded hillside, Middle Wheeling Creek, 6 mi. from mouth, July, 1937, *Bartholomew* 345 (WVU); Oglebay Park, May 4, 1929, *Strausbaugh* 46 (WVU); Hickory Hill, Wheeling, May 11, 1937, *West* 157 (WVU). MARSHALL CO.: bank of Fish Creek near mouth of Lower Bowman Run, June 15, 1940, *Bartholomew* 148 (WVU). MONONGALIA CO.: Morgantown, May 12, 1924, *Bourne* 45 (WVU); rich woods, Falling Run, Morgantown, May 2, 1890, *Millsbaugh* 75 (FM, NY, WVU); 1/2 mi. below Morgantown, May 16, 1937, *Myers* (WVU); Wadestown, *Thomas* (WVU). MARION CO.: College woods, May 9, 1937, *Beale* (WVU); near mouth of Pricketts Creek, May 16, 1937, *Harris* (WVU); rich shady moist woods, Rymer, May 15, 1937, *Thorn* (WVU). TAYLOR CO.: along Tygarts River, 2 mi. n. of Grafton, July 7, 1937, *Core* 5501 (WVU). BARBOUR CO.: dry mixed woods, east bank of Tygart Valley River, near Tygart Junction, Sept. 24, 1904, *Moore* 2564 (G, RM). UPSHUR CO.: Buckhannon, May 8, 1895, *Pollock* (M, US). PENDLETON CO.: 1 mi. n. of Mouth of Seneca, July 16, 1937, *Core* 6150 (WVU); eastern spur of the main ridge of the Alleghany Mts., above Horton, Sept. 17, 1904, *Greenman* 96 (G). RANDOLPH CO.: Pickens, Spring, 1938, *Perine* (WVU).

PLEASANTS CO.: near St. Marys, May 8, 1937, *Brooks & Margolin* (WVU). RITCHIE CO.: Mole Hill, Route 74, July 8, 1937, *Core 5611* (WVU); Cairo, Apr. 19, 1930, *Goodwin* (WVU). CALHOUN CO.: Pink, Apr. 22, 1933, *Harris* (WVU). KANAWHA CO.: rich shaded woods, around rock cliffs or old logs, Queen Shoals, Apr. 20, 1936, *Randolph 118* (WVU). CABELL CO.: near Lesage, May 1, 1937, *Brooks & Margolin* (WVU). FAYETTE CO.: near Glendale, May 1, 1937, *Brooks & Margolin* (WVU); Nuttallsburg, 1890, *Nuttall 46* (WVU). SUMMERS CO.: near Hinton, May 2, 1932, *Boone 60* (WVU); along stream, hollow of Hinton Mt., in horseshoe bend, May 4, 1939, *Tosh* (WVU). RALEIGH CO.: side of Baloff Mt., May 13, 1940, *Tosh 36* (WVU).

VIRGINIA. MADISON CO.: deep shade, s. and s. e. of Skyland, Shenandoah National Park, May 28, 1936, *Camp 1224* (NY). WYTHE CO.: shaded limestone bluffs, Wytheville, May 3, 1936, *Svenson 7767* (G). SMYTH CO.: Nicks Creek, vicinity of Marion, June 4, 1892, *Britton*, *Britton & Vail* (NY); Hungry Hollow, n. e. of Marion, May 24, 1892, *Small* (FM, M, MS); northeast slope of White Top Mt., May 28, 29, 1892, *Small* (FM); mouth of Hungrys Mother Creek, July 4, 1892, *Small* (FM, G, NY, US); Middle Fork of Holston River, Marion, July 6, 1892, *Small* (FM, M, WS).

TENNESSEE. SEVIER CO.: Le Conte, July 4, 1929, *Hudson* (RM).

NORTH CAROLINA. BUNCOMBE CO.: moist soil among rocks, Craggy Mt., May 15, 1898, *ex herb. Biltmore 751a* (G, M, NY, US); thick woods, vicinity of Montreat, Aug. 24, 1913, *Standley & Bollman 9993* (US).

GEORGIA. FLOYD CO.: Rome, *Ravenel* (M).

MICHIGAN. HURON CO.: rich yellow birch woods at base of cliff above Lake Huron, s. e. of Huron City, July 1, 1937, *Anderson & Peck* (WS). MIDLAND CO.: marshy thicket, 2 mi. s. of Midland, May 30, 1927, *Dreisbach 4771* (UM). GRATIOT CO.: Alma, May 16, 1891, *Davis* (MS, UM); Alma, May 26, 1892, *Davis* (UM). ST. CLAIR CO.: open sandy woods near Lake Port, and moist woods near Jeddo, June 30, 1937, *Anderson & Peck* (WS); rich woods near Port Huron, June 5, Aug. 14, 1892, *Dodge* (UM); Port Huron, May, 1888, *ex herb. Glatfelter* (M). OAKLAND CO.: Rochester woods, June 15, 1913, *Farwell 3472* (Farwell); Rochester, May 17, 1914, *Farwell 3624* (Farwell); Parke-dale Farm, June 13, 1915, *Farwell 3669* (Farwell, G, M, NY); Walled Lake woods, June 5, 1917, *Farwell 4487*, *4489* (Farwell), *4490* (Farwell, G); moist woods, Rochester waterworks, May 15, 1918, *Farwell 4819* (Farwell, G); Marl Lake woods, Sept. 18, 1920, *Farwell 5697* (Farwell); low wet ground, borders of woods, Walled Lake, June 5, 1917, *Farwell & Chandler 4488* (Farwell TYPE of *P. boreale* var. *multiflorum* Farwell); Birmingham, May 25, 1913, *Sutton 292* (UM). WAYNE CO.: woods, Detroit, May 9, 1895, *Farwell 380c* (Farwell), *380d* (Farwell TYPE of *P. boreale* var. *australe* Farwell); Palmer Park woods, Detroit, May 31, 1915, *Farwell 3951* (Farwell), *3952* (Farwell, G, M, NY); Mill Road woods, Redford, May 23, 1920, *Farwell 5447*, *5448* (Farwell, G), *5449* (Farwell); Livonia woods, May 21, 1929, *Farwell 8349* (Farwell); Detroit, June, 1870, *Foote* (UM). LIVINGSTON CO.: sandy soil, oak woods, Winants Lake, May 19, 1918, *Ehlers 685* (UM). WASHTENAW CO.: Ann Arbor, May 12, 1860, *ex herb. Almendinger* (UM); third woods, s. e. of Ann Arbor, May 13, 1925, *Emerson* (UM); moist ravine in oak woods, n. of North Lake, May 27, 1925, *Erlanson 1613* (UM); woods near Ypsilanti, May 21, 1891, *Farwell 380b* (Farwell); third woods, near Ann Arbor, May 17, 1926, *Hermann 106* (UM); low elm-oak woods, 5 mi. s. e. of Ann Arbor, July 14, 1935, *Hermann 6892* (FM, MS); Ann Arbor, May 28, *Lewis 73* (UM); Cascade Glen, Ann Arbor, May 24, 1915, *Romein* (UM). INGHAM CO.: woods n. of Agricultural College, May 21, 1894, *Skeels* (MS). JACKSON CO.: without exact locality, May 13, 1897, *ex herb. Camp & Camp* (FM). HILLSDALE CO.: Hillsdale, May 29, 1885, *ex herb. Pelton* (UM). MASON CO.: oak dune, Hamlin Lake, Ludington, Aug. 10, 1910, *Chaney 63* (C, FM, US). MUSKEGON CO.: swamp, Lake Harbor, May 28, 1898, *Umbach* (FM, US). KENT CO.: low rich soil, Grand Rapids, June 1, 1893, *Cole* (Minn); Orchid Swamp, Grand Rapids, May 16, 1897, *Fyfe & Shaddick* (MS). OTTAWA CO.: Holland, Aug., 1910, *Kauffman* (UM). BARRY CO.: Gun Lake, May 30, 1891, *Bailey* (UM). VAN BUREN CO.: ravine, n. of South Haven, Sept. 4, 1911, *Lansing 3334* (FM, G); along river and on wooded hillsides, South Haven, July 18, 1910, *Pennington* (UM). CASS CO.: Hemlock Island, Magician Lake, Aug., 1905, *Pepoon* (MS). BERRIEN CO.: climax forest, Warren Woods,

July 26, 1919, *Billington* (MS, UM), July 30, 1919, *Billington* (UM). CHEBOYGAN CO.: cut-over beech and sugar maple woods, Grapevine Point, Douglas Lake, July 12, 1919, *Deam* 28720 (D); same locality, July 19, 1921, *Ehlers* 1606 (UM); sandy soil, same locality, June 19, 1922, *Ehlers* 1945 (UM); Douglas Lake, July 20, 1911, *Gates* 372 (MS); in pineland aspens, Biological Station, July 3, 1917, *Gates & Gates* 10476 (M); Grapevine Point, Douglas Lake, July 9, 1929, *Hanna* 177 (RM). EMMET CO.: in hardwoods, w. of Pellston, June 22, 1917, *Gates & Gates* 10300 (FM, M, RM). CHARLEVOIX CO.: 4½ mi. n. w. of Vanderbilt, July 30, 1912, *Bessey* (MS). ANTRIM CO.: Bellaire, June 6, 1891, *Leavitt* (UM). ALGER CO.: rich deciduous woods above Miners Falls, near Munsing, July 2, 1934, *Fernald & Pease* 3240 (G); Chatham, Aug. 22, 1900, *Wheeler* (MS). MARQUETTE CO.: *Acer saccharinum* forest, Turin, May 31, June 5, 1901, *Barlow* (C, G, NY, US), Aug. 21, 1901, *Barlow* (G, MS, US TYPE of *P. cuneatum* Greene); Negaunee, June, 1902, *Rydberg* (NY). KEWEENAW CO.: Cliff Mine woods, June 20, 1886, *Farwell* 380, 380a, Oct. 1, 1914, *Farwell* 3909, July 3, 1915, *Farwell* 3995a, 3995b (Farwell); rich maple woods, 1 mi. w. of Mandan, July 10, 1936, *Hermann* 7917 (NY); hard maple woods, Lake Desor trail, Isle Royale, July 10, 1930, *McFarlin* 2154 (UM). HOUGHTON CO.: mixed woods, Lake Linden incline, July 5, 1934, *Farwell* 9893 (Farwell); Calumet waterworks, June 16, 1926, *Hermann* 277 (UM); St. Louis Hill, July 2, 1926, *Hermann* 456 (UM). ONTONAGON CO.: woods, south shore of Lake Superior, w. of Ontonagon, Aug., 1937, *Conard* (WS).

WISCONSIN. DOOR CO.: Ephraim, June 5, 1907, *Greenman* 2167 (M); Ephraim, May 30, 1926, *Kraus et al.* (G). BROWN CO.: cedar swamp, Green Bay, May 18, 1878, *Schuette* (FM); Upper Peninsula, Green Bay, June 14, 1889, *Schuette* (FM). WASHINGTON CO.: Hartford, June 1, 1929, *Quandt* (WS). MILWAUKEE CO.: Milwaukee, *Hasse* (NY); river bank, Wauwatosa, June, 1890, *Strong* (UM). WALWORTH CO.: Delavan, May, 1866, *Milligan* (US). SAUK CO.: wooded bank, Parfreys Glen, Merrimac, May 23, 1926, *Fassett* 3161 (G, NY). ONEIDA CO.: woods, Tomahawk Lake, Minocqua, Aug. 29, 1936, *Peck* (WS). CHIPPEWA CO.: woods, on red clay moraines, n. e. of Chippewa Falls, July 8, 1915, *Butters & Rosendahl* 3093 (Minn).

MINNESOTA. COOK CO.: maple forest, Mineral Center, July 5, 1924, *Rosendahl & Butters* 4592 (G, Minn, NY). BELTRAMI CO.: Cedar Island, Cass Lake, Aug. 2, 1914, *Pammel & Pammel* 575 (G). CLEARWATER CO.: loam, fir and birch woods, Schoolcraft Island, Itasca Park, July 30, 1929, *Grant* 2970 (G, Minn, US). HUBBARD CO.: *Populus tremuloides* forest, Benedict, Aug. 28, 1914, *Bergman* 3123 (NY, Minn). OTTERTAIL CO.: wet wooded places, Little Pine Lake, Perham, May 30, 1910, *Chandonnet* (D); Lake Lida, Aug., 1892, *Sheldon* 3760 (Minn). AITKIN CO.: Nichols, June, 1892, *Sheldon* 2107 (Minn). MILLE LACS CO.: Mille Lacs Indian Reservation, June, 1892, *Sheldon* 2532 (Minn). HENNEPIN CO.: rich woods, Minneapolis, May, 1892, *Burglebaus* (Minn); prairie, Fort Snelling Reservation, May 30, 1910, *Rosendahl* 2462 (Minn). WINONA CO.: Winona, June 9, 1888, *Holzinger* (US TYPE of *P. boreale* Greene); wooded bluffs, without locality, May, 1904, *Holzinger* (Minn).

OHIO. PORTAGE CO.: Newell Ledge, June 16, 1901, *Webb* 442 (G), May 10, 1903, *Webb* 609 (G). SUMMIT CO.: Peninsula, May 11, 1895, *Moseley* (FM). CUYAHOGA CO.: bank in woods, Berea, June, 1895, *Asbcroft* (RM); Berea, May, 1896, May, 1897, *Asbcroft* (M); Wade Park, Cleveland, May 14, 1912, *Dreisbach* 1030 (FM). LORAIN CO.: Oberlin, May 20, 1895, *Ricksecker* (US); rich moist woods, s. of Oberlin, May 21, 1892, *Strong* (UM). ERIE CO.: Cedar Point, May 19, 1893, *Moseley* (UM). OTTAWA CO.: Green Island, Aug. 20, 1940, *Myers* (WVU). RICHLAND CO.: rich damp soils, Mansfield, May 31, 1895, *Wilkinson* 10454 (Minn). FRANKLIN CO.: rich wooded hillsides, n. of Columbus, May 13, 1905, *Gleason* (G). CHAMPAIGN CO.: without locality or date, *Samples* (UM). CLARK CO.: Springfield, *Williams* (M). BUTLER CO.: uplands and ravines, Hueston woods, near Oxford, July 9, 10, 1924, *Wehmeyer & Waters* 86, 102 (UM).

INDIANA. STEUBEN CO.: low tamarack border of Graveyard Lake, ½ mi. from n. e. corner of state, May 25, 1920, *Deam* 30417 (D); black and white oak slope, e. side of Pokagon State Park, May 26, 1927, *Deam* 44289A (D); tamarack bog, ¼ mi. e. of Poka-

gon State Park, May 24, 1929, *Deam 46578* (D). LAGRANGE CO.: Sarah Long woods, along Pigeon River, 2 mi. w. of Mongo, May 17, 1915, *Deam 15702* (D); dry woods, 1½ mi. n. w. of Stroh, June 5, 1915, *Deam 15948*, *15957* (D); moist woods, 1½ mi. s. e. of Mongo, May 27, 1920, *Deam 30453* (D). DE KALB CO.: rich damp woods, 1 mi. s. of Garrett, May 17, 1908, *Deam 3034* (D); beech and sugar maple woods, 1 mi. s. of St. Joe, Aug. 17, 1916, *Deam 20849* (D); moist ground in beech and sugar maple woods, ½ mi. s. of St. Joe, May 25, 1920, *Deam 30383* (D); white oak ridge, 2 mi. s. e. of Hamilton, May 25, 1927, *Deam 44279* (D); Truelove woods, 3 mi. e. of Avilla, May 9, 1930, *Deam 48181* (D). NOBLE CO.: woods, 6 mi. s. w. of Rome City, June 20, 1910, *Deam 6780* (D); white oak woods, 4 mi. n. w. of Kendallville, June 6, 1915, *Deam 15848* (D). ALLEN CO.: white oak woods, ½ mi. s. of Viberg Lake, May 31, 1915, *Deam 15826* (Minn); moist woods, 4 mi. e. of Fort Wayne, May 31, 1915, *Deam 15832* (D, Minn). WHITLEY CO.: woods, 2½ mi. s. w. of Coesse, July 5, 1920, *Deam 31181* (D). ADAMS CO.: moist place, woods, 1 mi. w. of Ohio line, 5 mi. s. of Allen Co. line, Aug. 31, 1920, *Deam 32504* (D); rich moist woods of beech, elm and white oak, 3 mi. n. of New Corydon, May 13, 1921, *Deam 33814* (D). WELLS CO.: rich woods, near Bluffton, May 16, 1897, *Deam* (D, FM); rich woods, May 12, 1901, *Deam* (Minn, NY); woods, S. 30, Harrison Tp., May 14, 1905, *Deam* (M, US); Pearce woods, 1½ mi. n. w. of Craigville, Aug. 27, 1924, *Deam 40969* (D). HUNTINGTON CO.: moist woods, 2 mi. n. e. of Buckeye, May 26, 1907, *Deam 1946* (D, Minn); Colvin woods, 1½ mi. e. of Mt. Etna, May 8, 1934, *Deam 54781* (Minn). JAY CO.: beech woods, ¾ mi. n. of Bryant, May 18, 1916, *Deam 19733* (D); Cring woods, 2 mi. n. e. of Portland, July 19, 1923, *Deam 39130* (D); woods, S. 24, 2 mi. n. e. of Pennville, June 8, 1932, *Deam 52044* (D). BLACKFORD CO.: woods, S. 21, 4 mi. n. w. of Hartford City, June 5, 1932, *Deam 51974* (D). RANDOLPH CO.: woods, s. e. of Unionport, May 16, 1916, *Deam 19678* (D); beech woods, 5 mi. n. e. of Lynn, May 16, 1916, *Deam 19693* (D). DELAWARE CO.: woods, 5 mi. w. of Eaton, May 25, 1917, *Deam 23128* (D); same locality, May 27, 1921, *Deam 34086* (D). FAYETTE CO.: beech and sugar maple woods, 1 mi. s. e. of Alpine, May 17, 1921, *Deam 33059* (D); beech woods, 1 mi. n. e. of Orange, May 18, 1921, *Deam 34042* (D). RUSH CO.: woods, 1 mi. w. of Gowdy, May 1, 1922, *Deam 35340* (D); level rich woods, 2 mi. w. of Gowdy, July 7, 1925, *Deam 41395* (D). FRANKLIN CO.: Hillenbrand woods, 2 mi. n. w. of Hamburg, July 20, 1922, *Deam 36935* (D). RIPLEY CO.: woods, 1 mi. s. w. of Versailles, May 3, 1922, *Deam 35372* (D). JENNINGS CO.: beech-liquidambar-red maple woods, 7 mi. s. of Vernon, May 14, 1918, *Deam 24745* (D); red gum-red maple woods on the Frank Hite farm, 4 mi. s. e. of Vernon, Aug. 5, 1932, *Deam 52548* (D). OHIO CO.: wooded slope, along Laughery Creek, S. 5, 1½ mi. s. w. of Farmers Retreat, May 24, 1924, *Deam 40342* (D); wooded slope, along Laughery Creek, 3 mi. w. of Milton, May 9, 1929, *Deam 46567* (D); high wooded bluff, along Laughery Creek, S. 5, 3 mi. s. of Farmers Retreat, May 8, 1931, *Deam 49998* (D). ELKHART CO.: woods, 12 mi. n. w. of Goshen, May 11, 1916, *Deam 19576* (D); woods, 3 mi. s. of Middlebury, May 14, 1919, *Deam 27455* (D, G); black and white oak woods, 3 mi. s. w. of Middlebury, May 27, 1927, *Deam 44321* (D). ST. JOSEPH CO.: beech-white oak woods, 8 mi. w. of South Bend, May 10, 1916, *Deam 19540* (D); woods, 1¼ mi. s. e. of North Liberty, May 5, 1921, *Deam 33711* (D). KOSCIUSKO CO.: Plummer woods, 4½ mi. n. w. of Leesburg, May 14, 1923, *Deam 38271* (D); woods, 7 mi. n. e. of North Manchester, May 18, 1933, *Deam 53607* (D). MARSHALL CO.: woods, s. w. of Lake Maxinkuckee, May 20, 1901, *Clark 1676* (US); n. of Lapaz Junction, May 8, 1913, *Nieuwland 11035* (M). WABASH CO.: white oak, beech and sugar maple woods, 3 mi. n. e. of Disko, May 3, 1921, *Deam 33643* (D). MIAMI CO.: woods, 1 mi. e. of Deeds-ville, June 8, 1920, *Deam 31081* (D); low beech woods, Larison farm, 2½ mi. s. w. of Amboy, May 26, 1922, *Deam 36199* (D). CASS CO.: rich moist woods, 2½ mi. w. of Lucerne, June 9, 1931, *Deam 50242* (D). GRANT CO.: Leonard woods, 5 mi. n. w. of Upland, May 22, 1915, *Deam 15801* (D); Smith woods, 9 mi. e. of Marion, May 23, 1916, *Deam 19799* (D). HOWARD CO.: rich wooded bank of Wildcat Creek, 2 mi. w. of Greentown, May 15, 1910, *Deam 5947* (D). HAMILTON CO.: wooded hillside, e. of Carmel, May 11, 1913, *Deam 12677* (D). HANCOCK CO.: moist rich woods, 1½ mi. s. e. of Julietta, May 14, 1912, *Deam 10509* (D). MARION CO.: Decatur Tp., April 30,

1905, *Deam* (D). JACKSON CO.: rich beech woods, 1 mi. n. of Chestnut Ridge, April 25, 1910, *Deam* 5658 (D); wooded slope, Guthrie Creek, 6 mi. n. of Medora, May 15, 1918, *Deam* 24778 (D); wooded ravine, 2 mi. s. e. of Leesville, May 19, 1922, *Deam* 35751 (D). WASHINGTON CO.: with beech, base of wooded slope, 6 mi. s. e. of Pekin, S. 24, May 11, 1931, *Deam* 50018 (D). LA PORTE CO.: wooded sand dunes, w. of Michigan City, May 22, 1910, *Deam* 6427 (D); wooded dunes, e. of Michigan City, May 28, 1913, *Deam* 13046 (D); tamarack swamp, $\frac{1}{2}$ mi. n. of Mill Creek, June 4, 1920, *Deam* 30750 (D). CARROLL CO.: sugar maple woods, $1\frac{1}{2}$ mi. s. w. of Burnettsville, May 20, 1923, *Deam* 38314 (D); beech and sugar maple woods, $1\frac{1}{2}$ mi. w. of Camden, Aug. 17, 1925, *Deam* 42136 (D); wooded ravine, 5 mi. n. of Delphi, May 11, 1930, *Deam* 48238 (D). TIPPECANOE CO.: in ravines and on hillsides, along river road, La Fayette, May 5, 1900, *Dorner* (D). MONTGOMERY CO.: deep wooded ravines, Sugar Creek, near The Shades, May 16, 1913, *Deam* 12779 (D). PUTNAM CO.: woods at alluvial end of lateral ravine, D. P. U. arboretum, Greencastle, May 5, 1935, *Dawson* 1136 (Minn); wooded bank, Raccoon Creek, near McGaughey's, June 29, 1913, *Deam* 13479 (D); Nelson woods, 10 mi. n. w. of Greencastle, May 23, 1922, *Deam* 35974 (D); moist slope in woods, Knoll farm, S. 13, 4 mi. s. e. of Putnamville, May 17, 1926, *Deam* 42782 (D). MORGAN CO.: near Monroe Co. line, Monroe-Morgan State Forest, 6 mi. s. of Martinsville, May 22, 1930, *Deam* 48364 (D). OWEN CO.: with beech, woods, 3 mi. n. e. of Quincy, May 22, 1922, *Deam* 35906 (D). MONROE CO.: beech slope, 3 mi. n. w. of Harrodsburg, May 21, 1931, *Deam* 50167 (D); Fee pasture, $\frac{1}{2}$ mi. n. e. of Bloomington, 1908, *Pickett* (WS). LAWRENCE CO.: base of hemlock bluff, Back Creek, 2 mi. n. w. of Leesville, May 25, 1930, *Deam* 48441 (D). CRAWFORD CO.: wooded base of Evergreen Bluff, 4 mi. s. w. of Grantsburg, June 8, 1919, *Deam* 27792 (D, G.). PORTER CO.: Doran woods, 5 mi. s. w. of Lake Michigan, July 10, 1920, *Deam* 31487 (D); moist ground, north side of Doran woods, 4 mi. s. w. of Michigan City, May 23, 1923, *Deam* 38454 (D). FOUNTAIN CO.: moist woods, 2 mi. n. of Hillsboro, May 24, 1922, *Deam* 36037 (D). PARKE CO.: wooded ravine, Sugar Creek, near Turkey Run, Sept. 2, 1911, *Deam* 9917 (D). CLAY CO.: wooded bank of creek, 1 mi. e. of Harmony, May 4, 1914, *Deam* 12644 (D).

ILLINOIS. COOK CO.: damp woods, Forest Glen, June 4, 1892, *Harper* (WS); woods, near Chicago, June 4, 1892, *ex herb. Moffatt* 86 (Minn).

2. *Polygonatum cobrense* (Wooton & Standley) Gates in Bull. Torr. Bot. Club 44:126, *pl.* 6, B. 1917.

Salomonina cobrensis Wooton & Standley in Contrib. U. S. Nat. Herb. 16:113. 1913.

Perennial herb, 2 to 4 dm. high; rhizome slender; stem slender, somewhat flexuous, glabrous; leaves 10 to 12, alternate, more or less secund, elliptic, 4 to 9.5 cm. long, 0.9 to 3.2 cm. broad, obtuse or slightly acute, narrowed at the base to a broad petiole 3 to 4 mm. long, glabrous, glaucous beneath, very faintly nerved, only the midrib prominent; cauline bract papery, easily detached; peduncles strongly and sharply deflexed, flattened, glabrous, 8 to 15 mm. long, 1- or 2-flowered; pedicels 4 to 16 mm. long, glabrous, sometimes flattened; floral bracts white, papery, narrow, 3 to 6 mm. long, caducous; flowers fragrant, ivory-white, lobes and veins greenish; perianth of mature flower 17 to 23 mm. long, 7 mm. broad, tubular, somewhat expanded toward the mouth, the lobes erect, oblong, obtuse, nearly as long as the tube (about 7 mm. long); filaments slightly papillose, inserted near the middle of the tube; immature fruit pyriform, up to 8 mm. in diameter.

Polygonatum cobrense is easily distinguished from the other North American species. From *P. biflorum* and *P. commutatum* it differs in its papery, caducous

cauline bract and strongly deflexed peduncles. In these characters it resembles *P. pubescens*, from which it differs in its glabrous leaves, large flowers, slightly expanded cylindrical perianth tube, with the filaments inserted near the middle. It is very similar in appearance to the type species of the genus, the European *P. officinale*, and is possibly more closely related to this than to any North American species. Greene must have realized this relationship when he labelled some of his specimens from the Pinos Altos Mountains and Gila Canyon "*Polygonatum vulgare* Desf." [= *P. officinale* All.]—"New to America."

Specimens of *Polygonatum cobrense* were probably the basis for the inclusion of New Mexico and Arizona within the range of *Polygonatum commutatum* as given by Britton & Brown's 'Illustrated Flora' and others.

DISTRIBUTION: Sandy soil on north- and east-facing slopes, or in shade, mountains of Sierra and Grant counties, New Mexico, to southern Navajo County, Arizona.

NEW MEXICO. SIERRA CO.: shady places near Kingston, 1904, *Metcalf* 1036 (US). GRANT CO.: Copper Mines, Santa Rita, June, *Bigelow* (NY, US TYPE); Pinos Altos Mts., May 21, 1880, *Greene* 92 (G, M, NYCP); Gila Canyon, April, 1881, *Greene* (FM, G); shady loam, Mimbres River, south end of Black Range, 5500 ft. alt., July 1, 1904, *Metcalf* 1036 (FM, G, M, Minn, NY, US); sandy, usually rocky soil on north- and east-facing slopes or in shade, Canyon of Sapillo Creek, T. 4 or 5 S., R. 14 W., Gila National Forest, June 17, 1938, *Owney* & *Owney* 1643 (WS, to be distributed); grown at Pullman, Washington, from rhizomes of *Owney* & *Owney* 1643, June 10, 1944, *Owney* (WS, to be distributed); Copper Mines, 1851, *Wright* 1917 (G, NY, US).

ARIZONA. NAVAJO CO.: Ft. Apache, 1893, *Hoyt* (NY).

3. *Polygonatum biflorum* (Walter) Elliott, Sketch Bot. S. C. & Ga. 1:393. 1817.

Convallaria biflora Walter, Fl. Car., p. 122. 1788.

Polygonatum multiflorum γ. *biflora* Wood, Class-book of Bot., ed. 1, p. 396. 1845.

Salomonina biflora Farwell in Rept. Comm. Parks, Detroit 11:53. 1900.

Polygonatum angustifolium Pursh, Fl. Am. Sept. 1:234. 1814.

Convallaria angustifolia Sprengel, Syst. Veg. 2:96. 1825.

Convallaria canaliculata Mühlenberg in Willdenow, Hort. Berol. 1:45. 1806.

Polygonatum canaliculatum Pursh, Fl. Am. Sept. 1:234. 1814.

Polygonatum multiflorum δ. *canaliculata* Wood, Class-book of Bot., ed. 1, p. 396. 1845.

? *Convallaria parviflora* Poirlet in Lamarck, Encyc. Méth. Bot. Suppl. 4:29. 1816.

? *Polygonatum parviflorum* A. Dietrich in Otto & Dietrich, Allg. Gartenz. 3:222. 1835.

Polygonatum multiflorum β. *americanum* Hooker, Fl. Bor. Am. 2:176. 1839, probably in part.

Polygonatum biflorum var. *hebetifolium* Gates in Bull. Torr. Bot. Club 44:121. 1917, as to description mostly, and as to specimens cited except the type specimen ex herb. *Chapman* (pl. 5, A), and the specimen from Watson, Missouri, which is *P. commutatum*.

Polygonatum hebetifolium Bush in Am. Midl. Nat. 10:391. 1927, excluding name-bringing synonym.

Perennial herb up to about 6 dm. high; rhizome slender; stem slender, erect or arching, upper leafy part usually shorter than lower naked part; leaves alternate, sometimes secund, sessile to semiamplexicaul, elliptic-lanceolate, 4 to 11 cm. long, 0.9 to 3 cm. broad, the upper ones not much shorter than the lower ones, glabrous, paler and glaucous beneath, with 1 to 9 (usually 1 to 5) longitudinal nerves, only

the middle one prominent the entire length of the leaf, the others discernible but often hardly raised and usually fading out in the upper part of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, slender, glabrous, arcuate, 1- or 2 (rarely 3)-flowered; pedicels slender, glabrous, subequal, usually shorter than the peduncle; flowers whitish; perianth of mature flower 11 to 19 (usually 13 to 15) mm. long, 3 or 4 mm. broad in pressed material, cylindrical; perianth lobes 3 or 4 mm. long, scarcely spreading; filaments usually minutely papillose, inserted near the middle of the tube.

The type specimen of Walter's *Convallaria biflora* is preserved in the British Museum of Natural History. Dr. J. Ramsbottom, Keeper of Botany, has kindly sent a photograph of this specimen, accompanied by the following note by Mr. J. E. Dandy, Assistant Keeper:

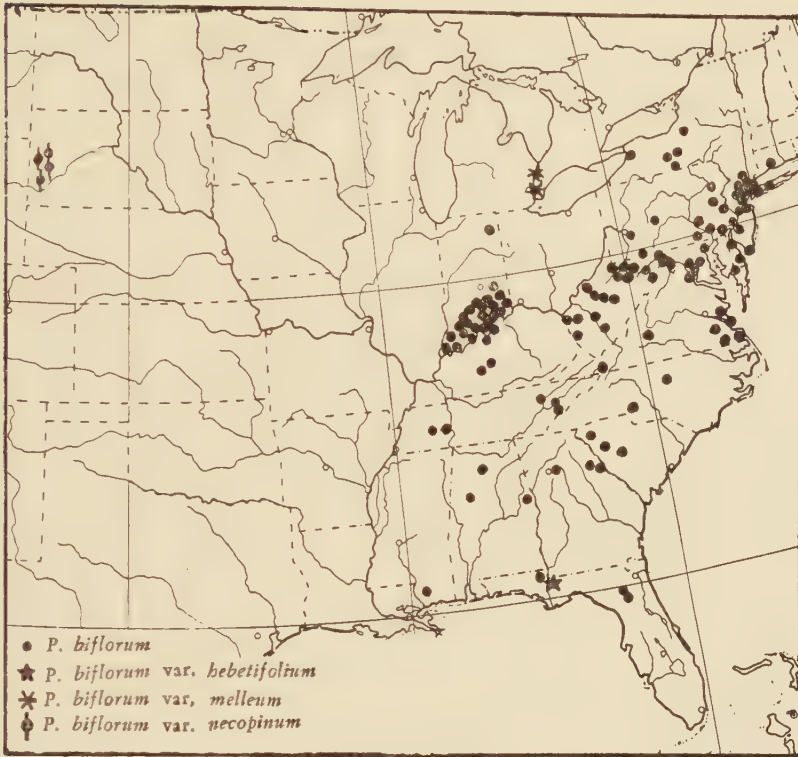
"The specimen is smooth and glabrous throughout (stem, leaves and peduncles). The leaves have dried brown, but the lower surface (as can be seen from the photo.) is paler and slightly glaucouscent.

"The specimen agrees with Walter's description except that the leaves are not markedly trinnerved. Flowers are absent, but they may have become broken off and lost. It is preserved on fol. 35 of Walter's Herbarium."

It is unfortunate that Gates did not see this specimen, for he misinterpreted Walter's species, considering the very narrow-leaved plants from the Chapman Herbarium (see *P. biflorum* var. *hebetifolium*) as typical. The specimens of the broader-leaved true *biflorum* which he saw, he included in his var. *hebetifolium*. It is because of this misinterpretation that Bush used the name *P. hebetifolium*, raising Gates' variety to specific rank, although the specimens he cited are probably all good *P. biflorum*.

As here interpreted, *Polygonatum biflorum* and its varieties compose the diploid element ($n = 10$) of the glabrous *P. biflorum*-*P. commutatum* complex of eastern North America. When all of the varieties of *P. biflorum* are considered together, the diploid element of the complex is indeed difficult to distinguish from the tetraploid element, *P. commutatum* ($n = 20$), except by chromosome number. In general, however, the diploids are smaller in size, daintier in texture, and have fewer and smaller flowers (except var. *hebetifolium*), and fewer prominent leaf nerves (except var. *melleum*); the upper leafy portion of the stem is usually shorter than or equal to the lower naked portion in length (except in var. *necopinum*). All members of the *P. biflorum*-*P. commutatum* complex are separated from the other two species in North America by the green, leaf-like, persistent cauline bract and by the arcuate, not strongly deflexed, peduncles.

The diploids are woodland plants and show little tendency to invade open places, roadsides, fence rows and alluvial soils. Geographically, *Polygonatum biflorum* is less widely distributed than the tetraploid species, and each of its three varieties is highly restricted in range. The present distributions of these four entities suggest that they are all remnants of a once widespread diploid. *P. biflorum* var. *melleum* is found in a small area in Michigan and Ontario, south of Lake Huron, and outside the range of *P. biflorum*. *P. biflorum* var. *hebetifolium* is known from only one locality in western Florida, within a small area which is



Map 2. Distribution of *Polygonatum biflorum* and its varieties. Based on Goode Base Map No. 102. By permission of The University of Chicago Press.

already famous for its other endemics, notably *Torreya taxifolia* and *Taxus floridana*. *P. biflorum* var. *necopinum* is restricted to the Black Hills of South Dakota, a region interesting because it is an outpost of the ranges of a number of species of plants, both eastern and western. *P. biflorum* itself, though found over a fairly wide area in eastern United States, also is limited in range. For the most part it is found south of the Wisconsin glacial drift. In Indiana, where the edge of that glaciation is well defined, the species lies wholly south of the boundary, except for a single collection from Allen County. Farther east, the layer of glacial drift is thinner, the boundary is less definite, and some collections from New York, Pennsylvania and Connecticut are apparently within the area of the Wisconsin glaciation.

DISTRIBUTION: Usually in sandy soil, moist to dry woods, Connecticut and New York, south to Florida, west to Indiana, Kentucky, Tennessee and Mississippi (Map 2).

CONNECTICUT. NEW HAVEN CO.: open ledges, top of West Rock, New Haven, June 24, 1932, *Eames 11429* (G).

NEW YORK. ORANGE CO.: Shunemunk Mt., near Mountainville, July 31, 1922, *Denslow* (NY). ROCKLAND CO.: Ramapo, May 24, 1922, *Denslow* (NY). WESTCHESTER

co.: near Bryn Mawr, May 21, 1893, *Bicknell 555* (NY); Larchmont, May, 1891, *Clarke* (NY). NEW YORK co.: "woods opp. Fire Engine House," New York, June 30, 1894, *Bicknell 557* (NY); Cactus Knoll, New York City, June 22, 1899, *Clute* (NY). SUFFOLK co.: hilly rich woods, n. of Motor Parkway, Wyandanch, June 2, 1925, *Ferguson 3762, 3763* (NY); hilly dry oak woods, Northport, May 21, 1927, *Ferguson 5447* (NY); dry hilly woods, Smithtown, June 9, 1927, *Ferguson 5572* (NY); dry hilly woods, Cold Spring Harbor, Aug. 31, 1926, *Ferguson 6013* (NY). NASSAU co.: woods, Merrick, May 27, 1921, *Ferguson 127* (NY); rich wet woods, Meadowbrook, June 10, 1925, *Ferguson 3786* (NY); edge of plains, East Meadowbrook, s. of Westbury and Hicksville, June 20, 1927, *Ferguson 5652, 5653* (NY); hilly rich woods, Locust Valley, June 7, 1928, *Ferguson 6590* (NY). QUEENS co.: high hilly woods, Queens, May 30, 1913, *Bicknell 558* (NY); Flushing, May 29, 1925, *Ferguson 3744* (NY). RICHMOND co.: Princes Bay, Staten Island, May 25, 1889, *Britton* (NY). ONONDAGA co.: Onondaga Valley, June, 1890, *Underwood* (NY). TOMPKINS co.: shore of Beebe Lake, Fall Creek Ravine and vicinity, Ithaca, May 27, 1915, *Alexander 3745* (G); cemetery, Ithaca, June 8, 1892, *Durand* (Minn); Fall Creek, June 9, 1893, *Schrenk* (M); dry ravine bank, between Renwick and McKinney's, Ithaca, June 18, 1916, *Wiegand 6198* (G). SCHUYLER co.: dry oak-cornel hillside, e. of Montour Falls, Montour, Sept. 23, 1917, *Wiegand 7886* (M). CHEMUNG co.: rich woods, without locality, June 3, 1896, *Lucy 2642* (FM). ERIE co.: Buffalo, *Clinton* (G). COUNTY NOT DETERMINED: South Harbor, June 9, 1895, *Howell* (M).

NEW JERSEY. BERGEN co.: moist woods, Carlstadt, 1877, *Oehler* (NYCP). PASSAIC co.: Boardville, Pompton, May 31, 1923, *Denslow* (NY); railroad embankment, near Hewitt, Sept. 17, 1923, *Denslow* (NY); Haskell, Pompton, June 6, 1927, *Denslow* (NY). MORRIS co.: woods, Chatham, May 30, 1903, *Mackenzie 189* (NY); dry woodlands, Budd Lake, June 9, 1918, *Mackenzie 8321* (NY). HUDSON co.: Snake Hill, near Hoboken, June 2, 1884, *Schrenk* (M). UNION co.: Plainfield, June 12, 1892, *Morong* (NY); Summit, June, *Slosson* (WS). MIDDLESEX co.: New Brunswick, May, 1894, *Blodgett* (NY); sandhills, Woodbridge, May 30, 1890, *Churchill* (G); New Brunswick, June, 1888, *Vail* (NY). MONMOUTH co.: Freehold, June 2, 1854, *Walters* (UM). MERCER co.: Pennington Mt., Hopewell, June 17, 1924, *Denslow* (NY). CAMDEN co.: rich thicket, e. of North Branch of Newton Creek at A. C. R. R., West Collingswood, May 22, 1926, *Adams 190* (M); thickets, Gloucester, May 30, 1922, *Dreisbach 2-83* (FM); roadside, Albion, June 7, 1926, *Meredith* (NY). GLOUCESTER co.: sandy fields and fence rows near the lighthouse, Washington Park, May 24, 1910, *Long 3509* (G). CAPE MAY co.: moist sandy woods, Cape May Point, June 3, 1928, *Benner* (G).

PENNSYLVANIA. MONROE co.: Naomi Pines, Pocono Plateau, June 7-10, 1889, *Britton* (NY). LEHIGH co.: woods, $1\frac{1}{8}$ mi. w. by s.w. of Wescosville, May 8, 1921, *Pretz 10665* (NY). BUCKS co.: woods, 2 mi. n.w. of Doylestown, May 31, 1925, *Dreisbach 3497* (UM); West Rockhill Tp., near Telford, June 13, 1926, *Strohm* (G). MONTGOMERY co.: Bryn Mawr, May, 1887, *Southworth* (UM). PHILADELPHIA co.: woods, East Fairmount Park, Philadelphia, May 17, 1877, *Redfield 8186* (M). CHESTER co.: West Chester, 1827, *Darlington* (NY); woods, Westtown Farm, May 24, 1905, *Wildman 172* (US). LANCASTER co.: Mountville, July, 1888, *Eby* (M); limestone, on the Little Conestoga Creek beyond Millersville, May 31, 1901, *Heller* (FM, G, US); limestone, woods below Graeffs Landing, Sept. 14, 1901, *Heller* (US); woods and thickets, Mountalto, June 6, 1906, 1908, *Illick* (M). DAUPHIN co.: woods, near Steelton, July 18, 1888, *Small* (FM). YORK co.: Conewago Creek, May, 1898, *Eisenhower* (M); without locality, June 3, 1895, *Glatfelter* (M); without locality, June 3, 1895, *Williams* (M). BLAIR co.: Rattlesnake Mt., Tyrone, Aug. 20, 1915, *Anderson* (G). WESTMORELAND co.: Shades Ravine, North Trafford, May 29, 1937, *Emig* (M). FAYETTE co.: woodlands, Ohiopyle, May 23, 1936, *Bright 13652* (WS).

DELAWARE. NEW CASTLE co.: woods, Townsend, May, 1890, *Canby* (Minn); Brandywine River, Wilmington, May 10, 1886, *Leeds* (FM). SUSSEX co.: dry sandy soil, without locality, Sept. 8, 1887, *Canby* (NY).

MARYLAND. WICOMICO co.: sandy woods, Salisbury, Aug., 1889, *ex herb. Canby* (NYCP). BALTIMORE co.: without locality, May 23, 1878, *Smith* (US). ALLEGANY

co.: Cumberland, 1894, *Sbriver* (NY). MONTGOMERY co.: rich rocky woods, near Widewater, below Greatfalls, May 10, 1916, *Kearney & Maxon* 77 (US); Cabin John Run, May 18, 1897, *Pieters* (UM); Glen Echo, May 19, 1895, *Pollard* 261 (US); damp woods, opposite Plummerts Island, May 9, 1915, *Standley* 11410 (US); Plummerts Island, in the Potomac River, near Cabin John, May 9, 1915, *Standley* 11473 (US). PRINCE GEORGES co.: Laurel, June 3, 1897, *Knowlton* (US); low woods at edge of swamp, e. of Sunnyside, June 7, 1918, *Maxon* 6420 (US).

DISTRICT OF COLUMBIA. Woods, Chevy Chase road, near Reno, May 25, 1904, *Chase* 2222 (FM, MS); in woods n. of Military Road, Rock Creek Park, May 25, 1915, *Maxon & Standley* 143 (US); Rock Creek Park, May 14, 1896, *Steele* (US); low ground, May 10, 1897, *Steele* (Minn); Piney Branch, May 9, 1895, *Topping* (Minn); Rock Creek, May 15, 1872, June 16, 1878, *Ward* (US); vicinity of Washington, Aug. 20, 1876, *Ward* (US).

VIRGINIA. ARLINGTON co.: Clarendon, May 25, 1928, *Blake* 10576 (WS); Fort Myer, May 14, 1896, *Mearns* (US). GLOUCESTER co.: vicinity of Capahosic, May 26, 1914, *Van Eseltine* 141 (US). JAMES CITY co.: rich soil of beech slope, 1/2 mi. w. of Williamsburg, May 11, 1920, *Grimes* 2577 (NY); deep wooded ravine, 2 mi. s.e. of Williamsburg, Apr. 21, 1921, *Grimes* 3472 (NY); rich wooded hillside, 1 mi. s.e. of Williamsburg, May 2, 1921, *Grimes* 3529 (G, NY). ELIZABETH CITY co.: damp thicket, Hampton, May 7, 1903, *Miller* (US). PRINCESS ANNE co.: rich woods, Great Neck, May 5, 1935, *Fernald & Griscom* 4356 (G); rich deciduous woods, e. of Little Creek, July 31, 1934, *Fernald & Long* 3857 (G); dry mixed woods, Little Neck, Aug. 8, 9, 1934, *Fernald & Long* 3858 (G); recently cleared sandy knoll, Virginia Beach, May 9, 1903, *Miller* (US). NORFOLK co.: near Norfolk, May 21, 1898, *Kearney* 1310 (US). SOUTHAMPTON co.: sandy alluvial bottomlands of Three Creek, Drewryville, June 22, 23, 1936, *Fernald, Long & Smart* 5718 (G). SUSSEX co.: sandy and loamy woods, s. of Pleasant Grove Church, July 22, 1936, *Fernald & Long* 6157, 6158 (G). BEDFORD co.: dry woods, without locality, May 10, 1871, *Curtiss* (G). SMYTH co.: vicinity of Marion, May 19, 1892, *Britton, Britton & Vail* (NY); slopes and summit of Pond Mt., East Marion, June 11, 1892, *Small* (FM).

WEST VIRGINIA. BERKELEY co.: Camp Frame, May 16, 1937, *Shreve* (WVU). MORGAN co.: summit of Cacapon Mt., July 9, 1937, *Core* 5783 (WVU). HAMPSHIRE co.: Hanging Rock, May 26, 31, June 15, 28, 1932, *Frye* 605, 540, 492, 1062a (WVU). MINERAL co.: Ridgeville, May 31, 1940, *Southern Appalachian Botanical Club Foray* (WVU). PRESTON co.: Lake Terra Alta, June 6, 1937, *Tighe, Conrad & Bergner* (WVU). MONONGALIA co.: Morgantown, May 31, 1926, *Humphrey* 788 (WVU). TAYLOR co.: Wendel, May 29, 1940, *Davis & Davis* 3970 (WVU). HARRISON co.: Shinnston, July 29, 1933, *Martin* 216 (WVU). WETZEL co.: woods, between Hundred and Littleton, June 9, 1931, *Haught* 349 (WVU). BRAXTON co.: Little Birch, June 1, 1933, *Harris* (WVU). CALHOUN co.: Sycamore, June 1, 1933, *Harris* (WVU). WIRT co.: 1 mi. above mouth of Reedy Creek, June 23, 1934, *Bartholomew* 94 (WVU). WOOD co.: Parkersburg, July 19, 1929, *W. V. U. Botanical Expedition* (G). KANAWHA co.: Gilligans Hill, May 30, Watts Hill, Aug. 9, 1934, *Greenlee* (WVU). LINCOLN co.: forest above Miller School, July 1, 1930, *Berkley* 907 (M). WAYNE co.: 1 mi. n. of Ft. Gay, Nov. 22, 1931, *Lycan* 13 (WVU). MINGO co.: Kermit, June 3, 1933, *Harris* (WVU). RALEIGH co.: along hollow, up Madams Creek, May 27, 1940, *Tosh* 118 (WVU).

NORTH CAROLINA. ORANGE co.: vicinity of Chapel Hill, May, 1898, *Ashe* (NY). MECKLENBURG co.: dry woods, Charlotte, Apr. 26, 1924, *Knowlton* (G).

SOUTH CAROLINA. ANDERSON co.: Watson woods, near Anderson, May 10, 1920, *Davis* 5102, 7021 (M), 7698 (UM); Norris farm, near Anderson, Aug. 7, 1919, *Davis* 9871 (M); dry oak woods, 6 mi. n. of Anderson, Aug. 20, 1927, *Wiegand & Manning* 804 (G). GREENWOOD co.: Greenwood, Aug. 24, *Davis* (M). LEXINGTON co.: vicinity of Batesburg, Apr. 29, 1911, *McGregor* 22 (US).

GEORGIA. RICHMOND co.: clay soil, ravine, Augusta, Apr. 25, 1903, *Cuthbert* (UF); ravine, Raes Creek, Augusta, Apr. 29, June 6, 1904, *Cuthbert* (UF). MCDUFFIE co.: wooded hillside near branch, vicinity of Thomson, Sept. 8, 1907, *Bartlett* 986 (UM),

Aug. 9, 1909, *Bartlett 1713* (D). DE KALB CO.: Stone Mt., May 1-18, 1895, *Small* (NY). FLORIDA. ALACHUA CO.: Buzzards Roost, Gainesville, May 3, 1936, *Arnold & West* (UF); same locality, May 2, 1928, *West* (UF). MARION CO.: McIntosh, Apr. 8, 1926, *Miller 532* (US). JACKSON CO.: hammock along Blue Springs, n. of Marianna, Mar. 17, 1937, *Exploration Party 1937* (UF); Chipola River, Marianna, July 20, 1936, *Hume* (UF).

ALABAMA. CULLMAN CO.: Cullman, Aug. 25, 1891, *Mobr* (US). TUSCALOOSA CO.: Tuscaloosa, Apr. 4, 1874, *ex herb. Mobr* (US); Tuscaloosa, Apr. 10, 1874, *Smith* (US). LEE CO.: Auburn, Apr. 17, 1897, *Earle & Baker* (NY); Auburn, Apr. 22, 1896, *Earle & Underwood* (NY).

MISSISSIPPI. HANCOCK CO.: Crane Creek, Apr. 3, 1918, *Johnson* (Farwell).

INDIANA. ALLEN CO.: wooded ravine, Robinson Park, 6 mi. n. e. of Ft. Wayne, June 3, 1906, *Deam 1054* (D). FAYETTE CO.: beech-sugar maple woods, 1 mi. s. e. of Alpine, May 16, 1921, *Deam 33939* (D). FRANKLIN CO.: Bane woods, 1½ mi. s. w. of Metamora, May 17, 1921, *Deam 33995* (D); Hillebrand woods, 2 mi. s. w. of Metamora, July 21, 1922, *Deam 36954* (D). DEARBORN CO.: beech-white oak woods, 3½ mi. s. e. of Sunman, May 19, 1919, *Deam 27561* (D); white oak-beech woods, 1 mi. s. w. of Farmers Retreat, May 24, 1924, *Deam 40352* (D). JENNINGS CO.: white oak woods, 2 mi. e. of Grayford, May 30, 1923, *Deam 38594* (D); woods, 3 mi. s. w. of Scipio, May 9, 1924, *Deam 40087* (D). JEFFERSON CO.: low flat woods, 2½ mi. n. e. of Kent, May 30, 1930, *Deam 48573* (D). SCOTT CO.: beech-sugar maple woods, 1 mi. n. of Lexington, May 20, 1919, *Deam 27585* (D, Farwell, G); beech woods, 1½ mi. n. of Lexington, May 5, 1922, *Deam 35422, 35439* (D); beech woods, along Kimberlin Creek, 4 mi. w. of Lexington, May 12, 1924, *Deam 40117* (D); beech slope, low woods of Chas. Shields, 1½ mi. w. of Lexington, May 15, 1927, *Deam 44241* (D). CLARK CO.: deep wooded ravine, just n. of tract 15, Clark Co. State Forest, May 11, 1910, *Deam 5864* (D); white oak woods, without locality, May 25, 1919, *Deam 27603* (Farwell). BARTHOLOMEW CO.: beech woods, 6 mi. n. w. of Columbus, June 5, 1921, *Deam 264* (D). BROWN CO.: woods, between Helmsburg and Nashville, May 21, 1910, *Deam 5983* (D); beech slope, 1 mi. w. of Georgetown [Bean Blossom], May 22, 1930, *Deam 48381* (D); white oak slope, 2 mi. e. of Helmsburg, May 22, 1930, *Deam 48386* (D). JACKSON CO.: wooded slope, south side of Guthrie Creek, 6 mi. n. of Medora, May 15, 1918, *Deam 24773* (D). WASHINGTON CO.: woods, Wright farm, 5 mi. s. e. of Salem, May 20, 1924, *Deam 40240* (D). HARRISON CO.: woods, 5 mi. s. e. of Milltown, June 25, 1915, *Deam 16434* (D); woods, 2 mi. n. e. of Corydon, June 3, 1917, *Deam 23384* (D); rich woods, 2½ mi. s. e. of Palmyra, June 4, 1917, *Deam 23424* (D); wooded slopes, Elizabeth, June 11, 1919, *Deam 27887* (Farwell); wooded slope of Elizabeth Hill, 3 mi. e. of Elizabeth, May 10, 1922, *Deam 35516* (D). MONROE CO.: beech woods, ¾ mi. n. w. of Harrodsburg, June 9, 1917, *Deam 23573* (D); woods, ½ mi. w. of Stanford, Aug. 8, 1918, *Deam 26072A* (D); wooded ravine, 11 mi. n. e. of Bloomington, May 21, 1922, *Deam 35851* (D); wooded sandstone slope, 3 mi. s. of Stanford, May 21, 1931, *Deam 50173* (D). GREENE CO.: sandy soil, sugar maple woods, 1 mi. n. of Newberry, July 3, 1918, *Deam 25659* (D). LAWRENCE CO.: woods, Donaldson farm, 3 mi. s. e. of Mitchell, July 12, 1915, June 8, 1917, *Deam 17282, 23525* (D); woods along Guthrie Creek, 1¼ mi. n. e. of Tunnelton, May 17, 1918, *Deam 24844* (D). MARTIN CO.: wooded cliff of White River, 2 mi. above Shoals, May 20, 1913, *Deam 12875* (D); wooded hillside, 2 mi. n. e. of Loogootee, July 10, 1915, *Deam 17140* (D). DAVIESS CO.: beech-white oak woods, 1 mi. n. e. of Portersville, June 11, 1929, *Deam 46831* (D); black and white oak ridge, 2 mi. n. e. of Corning, May 18, 1931, *Deam 50120* (D). ORANGE CO.: with beech, wooded slope, Meissen woods, 6 mi. s. e. of Paoli, May 14, 1922, *Deam 35652, 35668* (D). DUBOIS CO.: dry woods, 3½ mi. s. w. of Huntingburg, May 4, 1919, *Deam 27234* (D, Farwell); moist white oak woods, 3 mi. s. w. of Huntingburg, May 4, 1919, *Deam 27239* (D); crest of black and white oak woods, 2 mi. e. of Holland, May 29, 1926, *Deam 43050* (D). PERRY CO.: black and white oak woods, 7 mi. n. e. of Tell City, May 3, 1927, *Deam 44170* (D); with beech, base of a black and white oak slope, 6 mi. up Deer Creek from its mouth, May 6, 1929, *Deam 46546* (D); dry wooded slope, 5 mi. n. w. of Rome, Aug. 10, 1931, *Deam 50908* (D). WARRICK CO.: woods, 1½ mi. e. of New-

burg, June 11, 1918, *Deam* 25335 (D). GIBSON CO.: Mauck woods, 4 mi. s. e. of Princeton, June 30, 1918, *Deam* 25532 (D). POSEY CO.: very sandy woods, Dransfield farm, 3 mi. s. of New Harmony, Sept. 27, 1926, *Deam* 43841 (D).

KENTUCKY. JEFFERSON CO.: Louisville, 1835, *Short* (M). MEADE CO.: damp hillside by brook, Grahampton, near Fort Knox, Apr. 30, 1933, *Carleton* 245 (G). EDMONSON CO.: moist ravine, Chalybeate, May 8, 1936, *Shacklette* 309 (G). WARREN CO.: Bowling Green, May 29, 1899, *Price* (M).

TENNESSEE. KNOX CO.: rich wooded bluffs, Knoxville, June, 1897, *Ruth* 1172 (NY). BLOUNT CO.: Sunshine, June 5, 1929, *Hudson* 173 (RM). ROANE CO.: Oliver Springs, May 3, 1890, *Lamson-Scribner* (US). DECATUR CO.: without locality, May, 1855, *ex herb.* Ames (UM). MADISON CO.: rich woods, Jackson, May, 1892, *Bain* 307 (NY).

STATE NOT DETERMINED. Photograph of TYPE in the British Museum Herbarium (M).

3a. *Polygonatum biflorum* var. *melleum* (Farwell) R. Ownbey, n. comb.

Polygonatum melleum Farwell in Rept. Mich. Acad. Sci. 20:170. 1918.

Perennial herb, usually less than 6 dm. high; rhizome slender; stem slender, arching, upper leafy part usually about equalling lower naked part in length; leaves alternate, elliptic-lanceolate to short-elliptic, sessile to distinctly short-petiolate, 2.5 to 16 cm. long, 1 to 8.5 cm. broad, glabrous, dark green above, glaucous and paler beneath, with 5 to 11 nerves all of nearly equal prominence and all fading out above the middle of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, flattened, glabrous, arcuate, 2- to 4-flowered; pedicels unequal, equal to or shorter than the peduncle; flowers honey-yellow, 12 to 15 mm. long; filaments somewhat papillose to densely so, inserted near the middle of the perianth tube; immature berries up to 8 mm. in diameter.

Polygonatum biflorum var. *melleum* differs from *P. biflorum* in having many-nerved leaves, more and smaller flowers, and very nearly equal upper leafy and lower naked portions of the stem. The type specimen and plants like it may easily be distinguished also by the strikingly short and elliptic leaves, 2.1 to 2.5 times as long as broad, as opposed to 2.9 to 3.6 times in *P. biflorum*, and by a great difference in length between the lower and upper leaves of the same plant; in *P. biflorum* the lower leaves are usually 1.1 to 1.5 times as long as the upper ones; in typical var. *melleum* they are 2.1 to 2.4 times as long. A mass collection from the type locality of *P. biflorum* var. *melleum*, statistically studied, reveals, however, that this variety is extremely variable. Some individuals are indistinguishable from *P. biflorum*, while others are difficult or impossible to separate, on morphological criteria, from *P. commutatum*. Thus it cannot be considered to be a species.

DISTRIBUTION: Restricted to the region about Lake St. Clair, south of Lake Huron, in Michigan and Ontario (Map 2). At the type locality, at least, it is found on the beach of an ancient glacial lake.

MICHIGAN. ST. CLAIR CO.: open woods, glacial lake beach, near Algonac, June 30, 1937, *Anderson & Peck* (mass collection); open woods, Algonac, June 16, 1915, *Farwell* 3974 (Farwell TYPE); Algonac, Sept. 15, 1900, *Dodge* (UM).

ONTARIO. ESSEX CO.: Sandwich, July 25, 1901, *Macoun* 54099 (MS).

3b. *Polygonatum biflorum* var. *hebetifolium* Gates in Bull. Torr. Bot. Club 44:121, pl. 5, A. 1917, as to specimen cited as the type.

Polygonatum hebetifolium Bush in Am. Midl. Nat. 10:391. 1927, as to name-bringing synonym only.

Polygonatum biflorum sensu Gates in Bull. Torr. Bot. Club 44:120, pl. 4, B. 1917.

Perennial herb; stem simple, 4 to 5 dm. high, glabrous; leaves alternate, subsecund, semiamplexicaul, oblong-lanceolate, 5 to 9 times as long as broad, 6.5 to 13 cm. long, 0.8 to 2 cm. broad, the upper ones nearly as long as the lower ones, glabrous, with from 3 to 7 nerves of which only the middle one extends the full length of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, 12 to 35 mm. long, slender, glabrous, arcuate, 1- or 2-flowered; pedicels subequal, 3 to 15 mm. long, shorter than the peduncles, glabrous; flowers large, 20 to 23 mm. long, yellowish when dry; filaments minutely papillose, the free part shorter than the anthers.

Polygonatum biflorum var. *hebetifolium* is quite distinct from *P. biflorum* because of the long narrow leaves, 5 to 9 times as long as broad, the long slender flexuous peduncles, and the large flowers. It belongs, without question, to the *P. biflorum*-*P. commutatum* complex. Its morphological characteristics suggest that it is diploid, and as such it must be considered to be a variety of *P. biflorum*. The stomates, however, are even larger than is usual in the tetraploid *P. commutatum*. If it should be found to be tetraploid also, it must stand as a third species of this complex, taking the name *P. hebetifolium*. Attempts to secure living material for cytological study were unsuccessful. Mr. Leslie Hubricht looked for plants in its only known locality, and reported the native vegetation largely destroyed by wild pigs.

The only specimens of this variety known to the writer are several sheets from Chapman's herbarium in the Herbarium of the Missouri Botanical Garden. The one chosen by Gates as the type specimen has immature flowers and lacks data as to name of collector and place and time of collection. The other specimens include two sheets of plants collected in rich shady woods at Aspalaga, Florida, April, 1898, and a set of six sheets of very uniform specimens lacking collection data. These six are cited by Gates as typical of his conception of Walter's *Convallaria biflora*. Another sheet contains one specimen like those on the six sheets mentioned and one specimen with slightly broader leaves. This last plant Gates mentions in his discussion of the variety. All the other specimens cited by Gates with the original description are *P. biflorum*, except the plant from Watson, Missouri (*Bush* 527), which is *P. commutatum*. It is unfortunate that Gates selected one of the Chapman specimens to typify his variety *hebetifolium* when he referred the rest of them to *P. biflorum*. It is quite obvious that his intention was to separate the broad-leaved plants (true *C. biflora* Walter) as the variety, and it is to this broad-leaved element that the descriptive name "*hebetifolium*" (blunt-leaved) refers. Only the specimen which was designated as the type ties the inappropriate varietal name *hebetifolium* to the narrow-leaved entity.

Gates, for no apparent reason, except that Walter originally described *Convallaria biflora* in his 'Flora Caroliniana', states that the Chapman plants "doubtless came from somewhere in the southeastern states, probably North Carolina."

It seems much more likely that they were collected in western Florida, where Chapman lived, especially since two sheets in the group are so labelled.

DISTRIBUTION. Rich shady woods. Known from only one locality, along the Apalachicola River at Aspalaga, western Florida (Map 2).

FLORIDA. LIBERTY CO.: rich shady woods, Aspalaga, Apr., 1898, *ex herb. Chapman* (M). COUNTY NOT DETERMINED: without locality or date, *ex herb. Chapman* (M 138701 TYPE); without locality or date, *ex herb. Chapman* (M).

3c. *Polygonatum biflorum* var. *necopinum* R. Ownbey, n. var.⁴²

Perennial herb about 6 dm. high; rhizome slender; stem slender, nearly erect, upper leafy part longer than lower naked part; leaves alternate, short-petiolate, elliptic-lanceolate, 6.5 to 10 cm. long, 1.8 to 4 cm. broad, glabrous, paler and glaucous beneath, with 1 to 7 longitudinal nerves, only the midrib prominent the full length of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, slender, flattened, glabrous, arcuate, 2-flowered; pedicels slender, glabrous, subequal, shorter than the peduncle; flowers whitish, 15 to 17 mm. long, 5 or 6 mm. broad in pressed material, cylindrical, perianth lobes 4 mm. long, scarcely spreading; filaments nearly smooth, inserted near the middle of the tube.

Polygonatum biflorum var. *necopinum* is taller and has flowers a little larger than is usual in *P. biflorum*, and the upper leafy portion of the stem is considerably longer than the lower naked portion. Its habitat is on limestone rather than in sandy soil. Geographically it is found far outside the range of *P. biflorum*. Except for its diploid chromosome number it is very much like many plants of the tetraploid *P. commutatum*.

DISTRIBUTION. On limestone, deciduous woods along streams, foothills canyons of the Black Hills of western South Dakota (Map 2).

SOUTH DAKOTA. MEADE CO.: Black Hills, near Ft. Meade, July 27, 28, 1887, *Forwood* 348 (C, US). **LAWRENCE CO.:** Lead City, July 16, 1892, *Rydberg* 1039 (US). **PENNINGTON CO.:** Rapid Creek and Dark canyons, Rapid City, June 13, 1927, *Hayward* 821 (FM, RM); grown from rhizomes collected in Rapid Creek Canyon, 1 to 3 miles above Canyon Lake, moist shady slope under oaks and elms, limestone formation, June, 1939, *Ownbey & Ownbey* (M TYPE, WS). **CUSTER CO.:** in shade, along stream, State Game Lodge, June 26, 1924, *McIntosh* 408 (RM).

4. *Polygonatum commutatum* (Schultes f.) A. Dietrich in Otto & Dietrich, Allg. Gartenz. 3:223. 1835.

Convallaria commutata J. H. Schultes in Schultes & Schultes, Syst. Veg. 72:1671. 1830. *Polygonatum latifolium* var. *commutatum* Baker in Journ. Linn. Soc. [Lond.] Bot. 14:555. 1875.

Polygonatum biflorum var. *commutatum* Morong in Bull. Torr. Bot. Club 20:480. 1893; Mem. Torr. Bot. Club 5:115. 1894.

⁴² *Polygonatum biflorum* var. *necopinum*, var. nov. Herba perennis ad 6 dm. alta; radice subterranei; cauli subterranei prope erecto, parte superiori foliosa quam parte inferiori nuda longiori; foliis alternis brevi-petiolatis elliptico-lanceolatis, 6.5–10 cm. longis, 1.8–4 cm. latis, glabris, subtus pallidioribus glaucisque, 1–7-nerviis, medio-nervo solo prominente per totam longitudinem foliorum; bractea caulina viridi foliacea persistente; pedunculis axillaribus solitariis tenuibus compressis glabris arcuatis bifloris; pedicellis tenuibus glabris subaequalibus quam pedunculo brevioribus; floribus subalbidis, 15–17 mm. longis, 5 vel 6 mm. latis, cylindricis, laciniis 4 mm. longis leviter patentibus; filamentis subglabris, prope tubi medium insertis.

- Salomonina commutata* Farwell in Rept. Comm. Parks, Detroit 11:53. 1900.
Polygonatum latifolium Pursh, Fl. Am. Sept. 1:235. 1814, not *P. latifolium* (Jacq.) Desf. in Ann. Mus. Par. 9:50. 1807.
Polygonatum multiflorum *ε. latifolia* Wood, Class-book of Bot., ed. 2, p. 553. 1847.
Polygonatum giganteum A. Dietrich in Otto & Dietrich, Allg. Gartenz. 3:222. 1835.
Convallaria gigantea Hort. ex Dietrich, l. c., as synonym.
Polygonatum multiflorum *γ. giganteum* Wood, Class-book of Bot. Fl. U. S. & Can., p. 714. 1861.
Polygonatum canaliculatum *β. giganteum* Miquel in Ann. Mus. Bot. Lugduno-Batavi 3:148. 1867.
Polygonatum biflorum *β. giganteum* Wood, Am. Bot. and Flor., p. 346. 1870.
Polygonatum canaliculatum var. *giganteum* Farwell in Bull. Torr. Bot. Club 42:256, pl. 18. 1915; Am. Midl. Nat. 11:78. 1928.
Polygonatum multiflorum *β. americanum* Hooker, Fl. Bor. Am. 2:176. 1839, probably in part.
Polygonatum canaliculatum var. *americanum* Farwell in Bull. Torr. Bot. Club 42:256, pl. 17, B. 1915; Am. Midl. Nat. 11:77. 1928.
Polygonatum virginicum Greene, Leaflets 1:181. 1906.
Polygonatum biflorum virginicum Farwell in Bull. Torr. Bot. Club 42:254, pl. 15, B. 1915.
Polygonatum commutatum virginicum Gates in Bull. Torr. Bot. Club 44:123, pl. 6, A. 1917.
Polygonatum biflorum var. *ovatum* Farwell in Bull. Torr. Bot. Club 42:255, pl. 16, A. 1915.
Polygonatum commutatum ovatum Gates in Bull. Torr. Bot. Club 44:124. 1917.
Polygonatum ovatum Bush in Am. Midl. Nat. 10:397. 1927.
Polygonatum canaliculatum var. *ovatum* Palmer & Steyermark in Ann. Mo. Bot. Gard. 22:503. 1935.
Polygonatum ellipticum Farwell in Bull. Torr. Bot. Club 42:255, pl. 16, B. 1915.
Polygonatum commutatum var. *lineamentosum* Lunell in Am. Midl. Nat. 5:94. 1917.
Polygonatum canaliculatum var. *americanum* subvar. *ellipticum* Farwell in Am. Midl. Nat. 11:78. 1928.
Polygonatum canaliculatum var. *oblongifolium* Farwell in Rept. Mich. Acad. Sci. 22:181. 1921.
Polygonatum commutatum f. *ramosum* McGivney in Am. Midl. Nat. 9:664. 1925.
Polygonatum canaliculatum f. *ramosum* Clute in Am. Bot. 49:73. 1943.
Polygonatum biflorum f. *ramosum* Fernald in Rhodora 46:12. 1944.
Polygonatum biflorum var. *ovatum* subvar. *ellipsoidale* Farwell in Am. Midl. Nat. 11:78. 1928.

Perennial herb, 0.5 to 2 m. high, rarely smaller; rhizome stout, often branched; stem usually stout, arching, upper leafy part longer than lower naked part; leaves 11 to 25, alternate, amplexicaul, varied in shape, ovate-lanceolate, elliptic-lanceolate, oblong-lanceolate, or broadly oval, 6 to 18 cm. long, 1.5 to 10 cm. broad, glabrous, dark green above, glaucous and paler beneath, with 7 to 19, or more, major nerves, prominent the full length of the leaf, often so strong that the leaf is grooved on the upper surface, the major nerves alternating with other fainter, but distinct, nerves; cauline bract green, leaf-like, persistent; peduncles coarse, flattened, often stiff and wiry, usually long and arched, glabrous, 1- to 15-flowered; pedicels subequal to sometimes very unequal, usually shorter, but sometimes longer, than the peduncle; flowers yellowish green to greenish white, tipped with green, 14 to 23 mm. long, 3 to 7 mm. broad, perianth lobes more or less spreading; filaments smooth to densely papillose, inserted near the middle of the perianth tube; berries dark blue, 8 to 12 mm. in diameter.

Polygonatum commutatum represents the tetraploid element of the *P. biflorum*-*P. commutatum* complex. Although known under the name *P. commutatum* for nearly a century, this species has in recent years been passing under the name *P. canaliculatum*. During the early part of this work the latter name was mistakenly applied to this tetraploid element by the present writer. Since nearly all of the herbarium study was done at this time, specimens of *P. commutatum* in many herbaria were annotated as *P. canaliculatum*. A re-examination of the original description of *P. canaliculatum*, however, does not reveal a single character which will identify this description with the tetraploid species rather than with the diploid. The writer is now convinced that *P. canaliculatum* is completely synonymous with *P. biflorum*. It is hoped that anyone making use of her annotations will understand that specimens called "*P. canaliculatum*" are to be considered to be *P. commutatum*.

Although chromosome number is the only completely constant character which separates the two species of the complex, *P. commutatum* is usually distinguished by the greater vigor which often accompanies tetraploidy. These so-called *gigas* characters include a general robustness, a stouter stem, a larger number of leaves and flowers, broader and thicker leaves, coarser peduncles, larger flowers and fruits. *P. commutatum* usually differs from *P. biflorum* in its many-nerved leaves and in having the upper leafy portion of the stem longer than the lower naked portion. The former character occurs in *P. biflorum* var. *melleum*; the latter, in *P. biflorum* var. *necopinum*.

Geographically, *P. commutatum* is found not only over most of the area occupied by *P. biflorum*, but extends in nearly every direction beyond the range of the diploid species. As has previously been pointed out, the present distributions of *P. biflorum* and its varieties suggest that an ancestral diploid once extended at least as far west as the Black Hills of South Dakota. The several areas intervening between the remnants of this diploid have now largely been occupied by the more aggressive tetraploid.

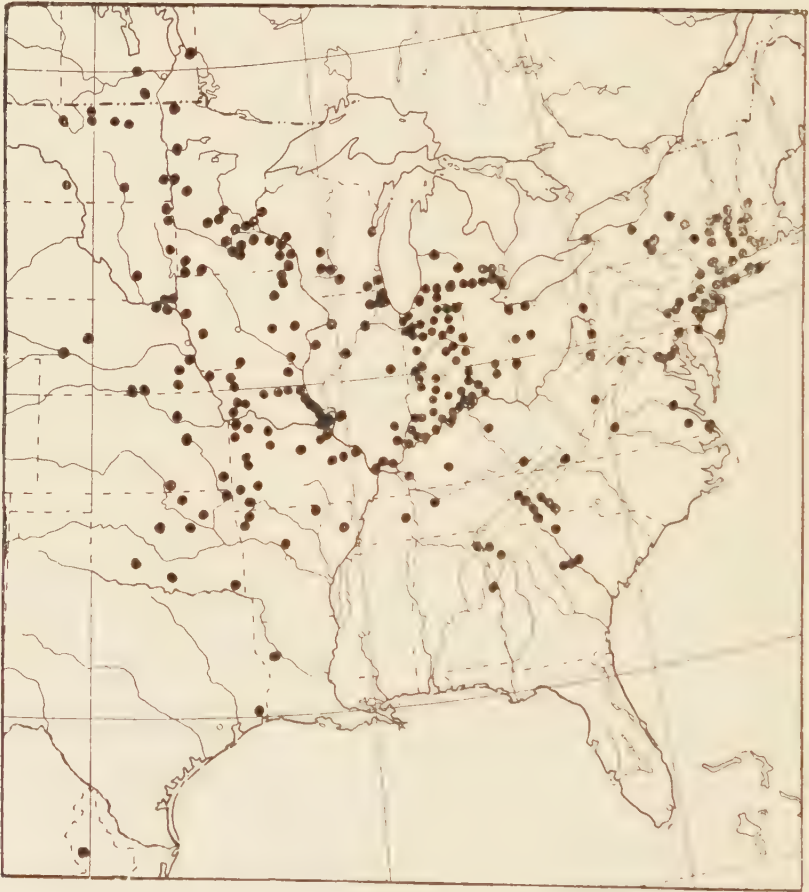
In unusually favorable habitats, in alluvial soils, along roadsides, and when cultivated, *P. commutatum* often reaches great size. It is this ecological type which Fernald⁴³ in his recent paper separated as the species, disregarding the fact that complete morphological intergradation exists between this extreme and the smaller, more slender ecotype of less favorable situations. The only certain way to distinguish small *biflorum*-like plants of *P. commutatum* growing within the distributional range of *P. biflorum* is by chromosome number. As explained in the section on cytology (page 377), there is no reliable way to estimate chromosome number in *Polygonatum* from herbarium sheets. Such fairly well-correlated characters as general vigor, size of leaves, number of flowers, and stomatal size and distribution, although very useful in this instance, fail to give a complete separation between the diploid and the tetraploid. It is therefore to be expected that the following list of exsiccatae will contain undetected diploids. Especially in the coastal region from New York to Virginia,

⁴³ Fernald, M. L. Specific distinctions between *Polygonatum biflorum* and *P. canaliculatum*. *Rhodora* 46:9-12. 1944.

in the mountains of North and South Carolina and Georgia, in Indiana and southern Michigan, the writer found plants which resembled *P. biflorum* except for their large size. Most of these questionable specimens were omitted from the citations of either species, although in most cases the specimens were annotated. It is hoped that the number of errors in citation and annotation will be small.

DISTRIBUTION. In sandy, calcareous, or alluvial soils, woods and open places; generally distributed throughout eastern North America from New Hampshire and Massachusetts, south to Georgia, west to the 102nd meridian from southern Manitoba to northeastern Mexico (Map 3).

ONTARIO. LINCOLN co.: dry soil, Dimming farm, near Niagara, June 16, 1884, *Macoun* (C). **WELLAND co.:** Point Abino, Lake Erie, Aug. 28, 1896, A. A. S. *Excursion* (NY); damp ravines, near Stamford, June 12, 1891, *Macoun* (C). **ESSEX co.:** Walkerville, June 9, 1891, *Johnson 10455* (Farwell); rich damp woods, Amherstburg, June 11, 1882, *Macoun* (C).



Map 3. Distribution of *Polygonatum commutatum*. Since the map was made, additional specimens from West Virginia, Indiana and Oklahoma have been seen. Based on Goode Base Map No. 102. By permission of The University of Chicago Press.

MANITOBA. ST. CLEMENTS DIST.: "Riviere Winipeg," July 14, 1857, *Bourgeau* (G). LAKESIDE DIST.: rich woods, Portage la Prairie, June 10, 1879, *Macoun* (C). MORDEN AND RHINELAND DIST.: by a brook, Morden, Aug. 4, 1896, *Macoun* (C).

NEW HAMPSHIRE. CHESHIRE CO.: Hinsdale, Aug. 2, 1902, *Blanchard* 80 (NY), 116 (G).

VERMONT. BENNINGTON CO.: bank of Hoosic River, Pownal, May 30, 31, 1900, *Eggleston* 2102 (G).

MASSACHUSETTS. HAMPSHIRE CO.: Southampton, *ex herb. Chapman* (M); bogs, Amherst, July 15, 1875, *Morong* (NY). HAMPDEN CO.: border of woods, slopes above the Connecticut River, Holyoke, Sept. 7, 1926, *Seymour* 602 (G, M, NY). BERKSHIRE CO.: Williamstown, June 29, 1901, *Churchill* (G); alluvial riverbank, Sheffield, June 12, 1919, *Churchill* (M); bank of Housatonic River, Stockbridge, June 9, 1912, *Kennedy* (G).

CONNECTICUT. NEW LONDON CO.: railroad grade, Franklin, July 25, 1911, *Woodward* (G). HARTFORD CO.: fence rows, Southington, June 29, 1898, *Andrews* 348 (G); dry border of field, Glastonbury, June 10, 1932, *Denslow* (NY); East Hartford, 1900, *Driggs* (G). MIDDLESEX CO.: Chatham, July 5, 1924, *Beals & Chamberlain* (NY). NEW HAVEN CO.: rich soil in copse, Milford, May 31, 1896, *Eames* (US); New Haven, June 5, 1884, *Safford* (US). LITCHFIELD CO.: Canaan, June 10, 1912, *Kennedy* (G). FAIRFIELD CO.: Stratford, July 23, 1871, *ex herb. Day* (NYCP); Fairfield, May 20, 1894, *Eames* (US); shrubby roadside on coast, Westport, Sept. 5, 1928, *Eames* 10779 (G); vicinity of Greens Farms, June 7, 1894, *Pollard* 41 (US).

NEW YORK. RENSSELAER CO.: Troy, 1828-1834, *Hall* (FM). ALBANY CO.: low moist woods, Wemple, Aug. 4, 1933, *House* 20625 (NY). GREENE CO.: Hotaling Island, Hudson River, New Baltimore, Aug. 19, 1909, *Taylor* 1395 (NY). DELAWARE CO.: Arkville, July 18, 1915, *Wilson* (NY). ULSTER CO.: Saugerties, May 28, 29, 1910, *Taylor* 1904 (NY). ORANGE CO.: Goshen, July 10, 1922, *Denslow* (NY); Tuxedo, June 12, 1892, *Morong* (NY); West Point, May 30, 1906, *Umbach* (NY). ROCKLAND CO.: Piermont, June 2, 1888, *Stabler* (G). BRONX CO.: McLeans Woods, Bronx, May 13, 1913, *Holtzoff* (NY); Bronx Park, May 25, 1896, *Nash* 140 (NY). SUFFOLK CO.: Orient, *ex herb. Farlow* (G); East Hampton, Oct. 16, 1919, *Ferguson A-1, A-2* (NY); hilly dry woods, Kings Park, Sept. 8, 1926, *Ferguson* 6055, 6056 (NY); openings in oak woods, Roanoke Point, Oct. 4, 1936, *Svenson* 8252 (G); copses, Northville, June, 1873, *Young* (FM). NASSAU CO.: Woodmere, June 11, 1916, *Bicknell* 560 (NY); dry level oak woods, Seaford, June 11, 1927, *Ferguson* 5606 (NY); dry oak woods, south edge of Hempstead Plains, East Meadowbrook, June 20, July 29, 1927, *Ferguson* 5650, 5940-a, 5940-c (NY); Inwood, June 10, 1888, *Poggenburg* (NY). QUEENS CO.: Queens, May 30, 1913, *Bicknell* 558a (NY); Springfield, Aug. 4, 1919, *Ferguson* (NY); Rosedale, July 27, 1926, *Ferguson* 5049 (NY); College Point, Sept., 1879, *Schrenk* (NY). RICHMOND CO.: Giffords, Staten Island, May 19, 1889, *Britton* (NY); Staten Island, June, 1868, *ex herb. Crooke* (NY). OTSEGO CO.: alluvial soil, open woods, banks of Cattaraugus Creek, Colliers, July 24, 1927, *Johnson* (NY). ONEIDA CO.: banks of Mohawk River, Utica, June 4, 1904, *Haberer* 922 (G). WAYNE CO.: Lyons, 1871, *Hankenson* (NY). TOMPKINS CO.: alluvial soil, Negundo Woods, Ithaca, July 6, 1920, *Muenschner & Bechtel* 114 (US, WS); valley of Inlet, Ithaca, June 24, 1915, *Thomas* 3751 (G); rich soil, corner of West Danby and Newfield state roads, Ithaca, June 11, 1919, *Wiegand* 11789 (M). SCHUYLER CO.: Cayuta Shops Flat, June 17, 1887, *Millsbaugh* (FM). CHEMUNG CO.: banks of large streams, without locality, June 11, 1894, *Lucy* 2643 (FM).

NEW JERSEY. SUSSEX CO.: Montague Tp., July 16, 1909, *Nash* (NY); Franklin, July, 1875, *Rusby* (UM); Peters Valley, June 1, 1895, *Van Sickle* (US). WARREN CO.: alluvial woods, Delaware River, Belvidere, June 5, 1921, *Mackenzie* (NY). BERGEN CO.: woods, Schraalenburgh, June, 1890, *Cutbbert* (UF); Carlstadt, June 1, 1884, *Niederer* (NYCP). HUDSON CO.: hills back of Hoboken, July, 1847, *without collector* (NY). ESSEX CO.: Millburn, Aug. 4, 1891, *Lightbipe* (NY). MIDDLESEX CO.: near Milltown, near New Brunswick, July 29, 1890, *Vail* (NY). MONMOUTH CO.: Pine Brook road, 2 or 3 mi. s. of Eatontown, Sept. 3, 1923, *Beals, Bassett & Sluyter* (G). BURLINGTON CO.: Kinkora, Aug. 18, 1910, *Taylor* 2544 (NY). CAPE MAY CO.: Avalon, June 15, 1925, *Leeds* (M). COUNTY NOT DETERMINED: S. Holland, July 18, 1914, *Miller* 1557 (NY).

PENNSYLVANIA. BUCKS CO.: George School woods, June 2, 1906, *Eves* (M); woods, 2½ mi. w. of Durham, Springfield Tp., Aug. 13, 1933, *Witte* (RM). MONTGOMERY CO.: without locality, *ex herb. Martindale* (G). PHILADELPHIA CO.: Philadelphia, *Morong* (M). DELAWARE CO.: meadows, without locality, June, 1861, *ex herb. Canby* (NYCP); moist soil, Chester Heights, Aston Tp., July 31, 1914, *Pennell 1613* (NY); Crum Creek, near Philadelphia, June 7, 1870, *Redfield 8187* (M). CHESTER CO.: without locality, June 5, 1882, *Fergus* (FM); Spread Eagle, June, 1870, *Martindale* (US). BERKS CO.: wooded hill, Moselem Springs, July 4-8, 1915, *Britton* (NY). LANCASTER CO.: Cone-wago, May, 1889, *Eby* (M); Reinholdsville, Aug. 26, 1889, *Small* (FM). BUTLER CO.: alluvial thickets along Connoquenessing Creek, Ribold, Sept. 18, 1932, *Bright 7761* (Minn), June 28, 1936, *13702* (WS). WASHINGTON CO.: rich woodlands along Mingo Creek, Old Distillery Station, May 28, 1938, *Bright 16324* (WS). COUNTY NOT DETERMINED: meadows, Avondale, June, 1896, *ex herb. Canby* (NYCP).

DELAWARE. NEW CASTLE CO.: New Castle, 1886, *ex herb. Tatnall* (G).

MARYLAND. HARFORD CO.: Spesutie Island, May 26, 1879, *Smith* (US). ANNE ARUNDEL CO.: without locality, May 29, 1878, *Smith* (US). PRINCE GEORGES CO.: between Seabrook and Buena Vista, May 31, 1915, *Maxon 6142* (US); wet woods along Sligo Branch, near the mouth, May 27, 1915, *Standley 11585* (US). MONTGOMERY CO.: Glen Echo, May 19, 1895, *Pollard 261* (US); damp woods, n. of Chevy Chase Lake, May 30, 1911, *Standley 5976* (US); Garrett Park, June 2, 1895, *Topping* (Minn).

DISTRICT OF COLUMBIA. Vicinity of Washington, June 12, 1878, *Chickering* (C, M); pine woods, Dalecarlia Reservoir, May 23, 1905, *Painter 1309* (M); High Island, May 10, 23, 1877, *Ward* (US); Fort Scott, May 15, 1879, *Ward* (US); Woodley Park, June 25, 1879, Sept. 18, 1880, *Ward* (US); alluvial soil, margin of large island, n. w. of Sycamore Island, May 12, 1918, *Wherry* (G, US).

VIRGINIA. PRINCESS ANNE CO.: rich woods, e. of Little Creek, May 4, 1935, *Fernald & Griscom 4355* (G). SUSSEX CO.: dry sandy hickory and oak woods, Burts, July 24, 25, 1936, *Fernald & Long 6155* (G). HENRICO CO.: Richmond, May 13, 1894, *Churchill* (G); Richmond, *De Chalmot* (US). BEDFORD CO.: banks of streams, without locality, June 5, 1868, *Curtiss* (FM); river bank and low rich woods, without locality, June 1, 1871, *Curtiss* (G). GILES CO.: Salt Pond Mt., June 1, 1890, *Brown, Hogg, Vail, Timmerman, Britton & Britton* (NY). SMYTH CO.: riverside, vicinity of Marion, May 22, 1892, *Britton, Britton & Vail* (NY); bluffs of Middle Fork Holston River, Marion, May 22, 1892, *Small* (FM, M, MS, US TYPE of *P. virginicum* Greene); along Nicks Creek, near base of Pine Glade Mt., June 2, 1892, *Small* (FM); south slope of White Rock Mt., June 21, 1892, *Small* (FM).

WEST VIRGINIA. HAMPSHIRE CO.: Hanging Rock, July 9, 1932, *Frye* (Minn). GREENBRIER CO.: White Sulphur Springs, July 16, 1892, *Brown* (NY). FAYETTE CO.: without locality, May 28, 1892, *Nuttall 788* (WVU). SUMMERS CO.: near Bellpoint, May 9, 1932, *Boone 93* (WVU). MONONGALIA CO.: Warm Hollow, July 8, 1939, *Davis & Davis 2746* (WVU); fence row, The Flats, June 4, 1890, *Millsbaugh 102* (NY, WVU); Dents Run, June 5, 1940, *Myers* (WVU). BROOKE CO.: along creek, Schubert farm, June 4, 1942, *Schubert* (WVU). OHIO CO.: damp woods, Nichols Hill, Wheeling, May 23, 1937, *Bartholomew 365* (WVU); near Bethany Pike, Oglebay Park, June 21, 1929, *Strausbaugh* (WVU). WETZEL CO.: Rocky Run, near Pine Grove, June 17, 1931, *Haught 439* (WVU). WIRT CO.: damp shaded bank of Little Kanawha River, ½ mi. above mouth of Reedy Creek, June 23, 1934, *Bartholomew 93* (WVU). CABELL CO.: bank of Guyan River, near junction of Russell Creek, June 19, 1937, *Gilbert 589* (WVU). LINCOLN CO.: Hamlin, May 28, 1933, *Harris* (WVU). WAYNE CO.: Dickson, May 12, 1931, *Gilbert 185* (WVU); Wayne, May 27, 1933, *Harris* (WVU); near Ft. Gay, May 7, 1932, *Lycan 17* (WVU).

NORTH CAROLINA. MADISON CO.: wooded slope, French Broad River, near Hot Springs, Aug. 14, 1924, *Webmeyer 638* (UM). BUNCOMBE CO.: river banks, Biltmore, May 20, 1896, *ex herb. Biltmore 1208* (Minn, RM, US). POLK CO.: rich woods, White-oak Mt., Columbus, July 21, 1921, *Peattie 1002* (G); side of Tryon Range, near Columbus, May 10, 1899, *Townsend* (WS). SWAIN CO.: vicinity of Swayney, Sept. 22, 1913, *Mooney* (US). MACON CO.: deep rich soil bordering water-courses, Highlands, May 25, 1897, *ex herb. Biltmore 1208b* (G, M, NY, US); Lake Satulah Falls, Highlands, June 8,

1901, Magee (G).

SOUTH CAROLINA. ANDERSON CO.: damp woods, Gluck Mill, Sept. 4, 1917, Davis 7194 (M, RM). AIKEN CO.: Aiken, July, 1869, Ravenel (US).

GEORGIA. RICHMOND CO.: island in Savanna River, 16 mi. above Augusta, April 27, 1904, Cutbberth 1090 (UF). MCDUFFIE CO.: woods, 2 mi. w. of Thomson, Sept. 17, 1908, Bartlett 1417 (UM). COBB CO.: small knob, Kennesaw Mt., May 12, 1934, Perry & Myers 822 (G, NY). FLOYD CO.: cliffs of the Coosa River, 1872, Ravenel (M).

ALABAMA. DEKALB CO.: shaded rocky banks, Lookout Mt., 1900 ft. alt., Hotel de Kalb, Mentone, June 4, 1892, Mohr (US). LEE CO.: Auburn, May 8, 1897, Earle & Baker (NY).

MICHIGAN. MACOMB CO.: Washington, Cooley (MS). OAKLAND CO.: Parkedale Farm and Rochester, various dates, 1912 to 1917, Farwell 2983, 3473, 3673 TYPE of *P. ellipticum* Farwell, 3674, 3675, 3676, 3677, 3677½, 3678, 3679, 3682 TYPE of *P. canaliculatum* var. *oblongifolium* Farwell, 3683, 3681½, 4236a, 4237a, 4508½ TYPE of *P. biflorum* var. *ovatum* subvar. *ellipsoidale* Farwell (Farwell; several of these numbers also at G and NY, but localities or dates not always corresponding). WAYNE CO.: Detroit, near Mich. So. R. R., June 25, 1871, ex herb. Boott (G); woods on Belle Ile, June 8, 1893, Farwell 1150a (Farwell TYPE of *P. biflorum* var. *ovatum* Farwell); open dryish fields, Rockwood, June 24, 1916, Farwell 4234 (Farwell), 4235 (Farwell, G). WASHINGTON CO.: Ann Arbor, June 15, 1860, Almendinger (UM); bank of Huron River, w. of Ann Arbor, June 30, 1924, Erlanson 120 (UM); woods, near Ypsilanti, June 13, 1891, Farwell 1150 (Farwell); moist wooded hillside, left bank of Huron River, just above city beach, Ann Arbor, Aug. 20, 1924, Gustafson & Best (UM); edge of low woods, Nichols Arboretum, Ann Arbor, June 30, 1935, Hermann 6832-a, 6832-b (FM, MS), 6832-c (FM); Cedar Bend, Ann Arbor, July 12, 1915, LaRue (UM); Huron River Terr., Ann Arbor, June 7, 1903, Thomson (UM); woods, w. of Ann Arbor, June 23, 1838, ex herb. Thurber (G); near Ypsilanti, June 15, 1870, Whitney (UM). INGHAM CO.: Agricultural College, June 16, 1887, Cooley (MS); bank of Red Cedar River, Agricultural College, June 26, 1895, Skeels (MS); moist open woods, Lansing, June 7, 1917, Yuncker 184 (US). JACKSON CO.: 3 mi. e. of Hanover, June 28, 1937, Anderson & Peck (WS). CALHOUN CO.: s. of Marshall, Aug. 2, 1898, Beal (MS). KENT CO.: Grand Rapids, June 27, 1892, July 7, 1893, Bailey (UM); Grand Rapids, June, 1886, Crozier (NY, US); Grand Rapids, Aug. 21, 1935, Rusby (NY). KALAMAZOO CO.: shady spot, roadside, Schoolcraft, June 6, 1903, Burgess 55 (FM); in lane leading to lake, Sugarloaf Lake, June 16, 1903, Burgess 155 (FM); roadside, Schoolcraft, Sept. 30, 1903, Burgess 397 (FM); fence row, Sugarloaf Lake, Oct. 3, 1903, Burgess 460 (FM). ST. JOSEPH CO.: between Mud Lake and Clear Lake, June 27, 1937, Anderson (WS); Constantine, June 9, 1903, Davis (WS). VAN BUREN CO.: South Haven, July 6, 1910, Pennington (UM); wooded bank, Keeler, 1906, Pepoon 763 (MS). BERRIEN CO.: flood plain, Warren Woods, May 18, 1921, Billington (UM).

OHIO. WAYNE CO.: Wooster, July 4, 1907, Laughlin 970 (G). LORAIN CO.: woods, Oak Point, June 8, 1895, Ricksecker (US). ERIE CO.: Cedar Point, May 29, 1894, Moseley (M). RICHLAND CO.: waste ground, without locality, June 20, 1892, Wilkinson (Minn). FRANKLIN CO.: Columbus, May 30, 1898, Colevenger (US). CHAMPAIGN CO.: near Urbana, June 23, 1838, without collector (UM). CLARK CO.: Springfield, Williams (M). BUTLER CO.: moist woods, Oxford, June 22, 1910, Overholts (M). HAMILTON CO.: edge of woods, Mt. Airy Forest, Cincinnati, June 8, 1931, Stephenson (RM).

INDIANA. STEUBEN CO.: middle of high wooded black oak slope, north side of Cheeseboro Lake, S. 19, 3½ mi. n. w. of Angola, June 22, 1937, Deam 57888 (D); woods, near Lake Gage, June 16, 1903, Deam (D). LAGRANGE CO.: white oak woods, 3 mi. e. of Howe, June 5, 1915, Deam 15911 (D); woods, north side of Cedar Lake, June 12, 1916, Deam 20180 (D); base of sandy black oak slope, 1 mi. s. of Mongo, Sept. 14, 1918, Deam 26335 (D); black and white oak woods, 1½ mi. s. e. of Mongo, July 13, 1923, Deam 39093 (D); in sphagnum, tamarack bog along Pigeon River, 1½ mi. s. e. of Mongo, June 17, 1937, Deam 57860 (D). NOBLE CO.: dry woods, 4 mi. s. e. of Ligonier, June 26, 1914, Deam 14346 (D); moist woods, 5 mi. s. w. of Albion, Aug. 25, 1914, Deam 14697 (D); sandy soil, school-house grounds, north side of Blackman Lake,

1 mi. e. of Kimmel, July 1, 1924, *Deam 40789* (D). WHITLEY CO.: black and white oak woods, north side of New Lake, 9 mi. n. w. of Columbia City, July 1, 1924, *Deam 40779* (D). ADAMS CO.: without locality, Aug. 1, 1900, *Kauffmann* (UM). HUNTINGTON CO.: bank of Salamonie River, 3 mi. n. w. of Warren, Aug. 15, 1924, *Deam 40948* (D). JAY CO.: woods, Godfrey Indian Reserve, S. 20, 3 mi. n. w. of Pennville, June 11, 1931, *Deam 50258* (D). DELAWARE CO.: river bank, 1 mi. e. of Eaton, June 4, 1911, *Deam 8532* (D). WAYNE CO.: woods, $3\frac{1}{2}$ mi. n. w. of Richmond, June 4, 1913, *Deam 13136* (D). UNION CO.: wooded ravine, 3 mi. s. of Liberty, June 16, 1915, *Deam 16006* (D). DECATUR CO.: along a fence along a woods, 5 mi. s. of Greensburg, May 31, 1921, *Deam 34171* (D). DEARBORN CO.: wooded ravine, $\frac{1}{2}$ mi. w. of Aurora, June 17, 1915, *Deam 16038* (D); wooded bank of Laughery Creek, 4 mi. w. of Aurora, June 18, 1915, *Deam 16109* (D). RIPLEY CO.: wooded hillside along Laughery Creek, just e. of Versailles, July 23, 1913, *Deam 13789* (D). JENNINGS CO.: wooded area, 5 mi. s. e. of Vernon, May 22, 1942, *Friesner 16681* (WS). SWITZERLAND CO.: wooded hillside, just n. of Vevay, July 25, 1913, *Deam 13824* (D). JEFFERSON CO.: Hanover, June 17, 1874, *Coulter* (FM). CLARK CO.: without locality, May 6, 1851, *Mohr* (US). ELKHART CO.: woods, river bank, $\frac{1}{2}$ mi. n. of Middlebury, June 4, 1912, *Deam 10966* (D). MARSHALL CO.: Long Point, near Lake Maxinkuckee, June 17, 1901, *Clark 1774* (NY, US); woods, south side of Lake Maxinkuckee, Sept. 14, 1921, *Deam 34769* (D); Lake Maxinkuckee, Aug. 8, 1899, *Evermann 950* (US). FULTON CO.: woods along Tippecanoe River, just n. of DeLong, June 7, 1920, *Deam 30082* (D). MIAMI CO.: border of woods, 1 mi. n. w. of Denver, June 30, 1922, *Deam 36797* (D). GRANT CO.: woods, 2 mi. n. e. of Van Buren, June 16, 1907, *Deam 2049* (D). JACKSON CO.: slope of wooded beech ravine, 1 mi. w. of Medora, July 15, 1919, *Deam 28129* (D). FLOYD CO.: base of wooded slope, 2 mi. w. of New Albany, June 13, 1919, *Deam 27931* (D). HARRISON CO.: near base of wooded slopes, Falling Springs Hollow, 3 mi. e. of Elizabeth, June 1, 1917, *Deam 23336* (D). STARKE CO.: black oak woods, 6 mi. n. e. of North Judson, June 27, 1930, *Deam 49007* (D). PULASKI CO.: wooded bank, Tippecanoe River, $3\frac{1}{2}$ mi. n. e. of Winamac, June 9, 1923, *Deam 38831* (D). WHITE CO.: black oak clearing, $2\frac{1}{2}$ mi. s. of Lee, Sept. 17, 1921, *Deam 34906* (D). TIPPECANOE CO.: woods, $1\frac{1}{2}$ mi. n. e. of Romney, May 25, 1922, *Deam 36063* (D). BOONE CO.: roadside, 4 mi. n. of Lebanon, June 19, 1943, *Friesner 17749* (WS). HENDRICKS CO.: wooded creek bottom, White Lick River, June 22, 1912, *Deam 11236* (D). PUTNAM CO.: woods, 2 mi. s. w. of Morton, Aug. 24, 1922, *Deam 37821* (D); Greencastle, May, 1893, *Underwood* (NY). MORGAN CO.: low wooded bank, White River, $1\frac{3}{4}$ mi. s. e. of Paragon, May 21, 1922, *Deam 35866* (D). MONROE CO.: near "Phi Delta" house, Bloomington, June 7, 1923, *Hawkin* (UF). GREENE CO.: along railroad, $\frac{1}{2}$ mi. e. of Bushrod, May 26, 1912, *Deam 10682* (D). LAWRENCE CO.: wooded bluff, [East Fork of] White River, $\frac{1}{4}$ mi. e. of Tunnelton, May 16, 1918, *Deam 24812* (D). DAVIESS CO.: wooded bank, [East Fork of] White River, just e. of the Portersville Bridge, July 17, 1919, *Deam 28221* (D). CRAWFORD CO.: roadside, $\frac{1}{2}$ mi. s. of Marengo, June 7, 1919, *Deam 27777* (D, G); wooded slopes, Grantsburg, June 9, 1919, *Deam 27801* (Farwell). PERRY CO.: wooded bluff, Ohio River, 5 mi. e. of Cannelton, June 29, 1915, *Deam 16626* (D). SPENCER CO.: dry woods, 3 mi. w. of Troy, June 30, 1915, *Deam 16656* (D). WARRICK CO.: high wooded bank, Cypress Creek, 2 mi. e. of Newburg, June 11, 1918, *Deam 25301* (D). PORTER CO.: woodlands, without locality, June 28, Aug. 11, 1929, *Buhl 103* (FM). LAKE CO.: north slope, low wooded dune, $\frac{1}{2}$ mi. e. of East Gary, June 10, 1922, *Deam 30458* (D); sandy wooded ridge, $2\frac{1}{2}$ mi. n. w. of Hobart, July 18, 1931, *Deam 50553* (D); rich woods, Valparaiso, May 23, 1900, *Lansing 824* (FM); dry sandy woods, Clarke, Sept. 3, 1903, *Lansing 1840* (FM). JASPER CO.: black oak sand hill, 5 mi. w. of Gifford, July 14, 1920, *Deam 31706* (D). FOUNTAIN CO.: along creek, near Veedersburg, June 5, 1905, *Deam* (D); on crest of white and black oak ridge, Portland Arch Park, near Fountain, Aug. 15, 1932, *Deam 52835* (D). KNOX CO.: wooded border of Claypool Pond, 15 mi. s. w. of Decker, July 8, 1915, *Deam 17000* (Minn). GIBSON CO.: woods, Gordon Hills, 6 mi. w. of Patoka, July 6, 1915, *Deam 16905* (D). POSEY CO.: wooded ravine, 4 mi. s. of Mt. Vernon, May 24, 1911, *Deam 8322a* (D).

KENTUCKY. HARLAN CO.: top of Big Black Mt., near state line, June 17, 1936, *Camp 1492* (NY). SCOTT CO.: Elkhorn Cliff, Stamping Ground, May 12, 1930, *Singer* (US). WARREN CO.: Bowling Green, June, 1899, *Price* (M). LYON CO.: Kuttawa, June 2-18, 1909, *Eggleston 4579* (NY). COUNTY NOT DETERMINED: moist shady thicket, Elk Lick Falls, May 19, 1923, *McFarland 99* (M, US).

TENNESSEE. SEVIER CO.: rocky ravine, Elkmont, July 29, 1924, *Wehmeyer 378* (UM). KNOX CO.: woods, Knoxville, April, May, 1898, *Ruth 140, 735* (US), *147, 749* (NY), *148, 781* (M). CHEATHAM (?) CO.: limestone of Harpeth River, w. of Nashville, May 17, 1934, *Harger 7807A* (G). HENDERSON CO.: moist sandy hillsides, near Lexington, May 20, 1920, *Palmer 17575* (M).

WISCONSIN. BROWN CO.: DePere, June 23, 1888, *Kellogg* (US); Wrightstown, Aug. 17, 1879, *Schuette* (FM); Bellevue Creek, June 13, 1880, *Schuette* (FM); Fort Howard, June 18, 1881, *Schuette* (G); copses, Fort Howard marsh, June 26, 1886, June 26, 1887, *Schuette* (FM); Kellogg stockfarm, Allouez, June 27, 1897, *Schuette* (FM, NY); Green Bay, June 22, 1898, *Schuette* (FM). RACINE CO.: Racine, Sept. 11, 1879, *Davis* (M). WALWORTH CO.: Lake Geneva, Ayer (FM); vicinity of Delavan, July 11, 1919, *Hollister 43* (US); 1½ mi. n. w. of Lake Geneva, 1885, *Scoville* (RM). DANE CO.: Madison, Aug. 25, 1893, *Churchill* (G). SAUK CO.: woods, Mirror Lake, July 13, 1903, *Eggert* (M). RICHLAND CO.: rich soil, wooded hillside, ½ mi. e. of Richland Center, June 7, 1912, *Lansing 3421* (FM). JUNEAU CO.: Camp Douglas, July 16, 1890, *Mearns 666* (US). BUFFALO CO.: near Fountain City, *Finkelnburg* (Minn). POLK CO.: St. Croix Falls, July 18, 1900, *Baker* (G).

ILLINOIS. LAKE CO.: beach, n. of Waukegan and e. of the glacial Glenwood Ridge, June 16, 1909, *Gates 3025* (UM). COOK CO.: edge of woods, Palos Park, May 24, 1913, *Johnson* (NY); woods, near Chicago, June 30, 1892, June 29, 1891, *Moffatt 171, 329* (Minn); Stony Island, June 25, 1914, *Smith 5932* (G, M). DU PAGE CO.: railroad, Lisle, June 4, 1918, *Martinek 191* (US); woods, Naperville, May 9, 1895, *Umbach* (Minn), May 21, 1895, *Umbach* (US), June 16, 1898, *Umbach 1040* (G). KANE CO.: shaded ground, Bliss Woods, 7 mi. w. of Aurora, July 30, 1925, *Erlanson 1547* (UM). LA SALLE CO.: rich shady woods, Starved Rock, June 1-7, 1909, *Greenman, Lansing & Dixon 9* (G, NY). PEORIA CO.: moist woods, Peoria, June, 1904, *McDonald* (G). ROCK ISLAND CO.: Port Byron, Aug. 11, 1892, *ex herb. Harper* (WS). HENDERSON CO.: moist shaded sand dunes, Oquawka, July 7, 1908, *Gleason* (G). CHAMPAIGN CO.: shady bank, Crystal Lake, Urbana, May 23, 1911, *Pease 13090* (G). RICHLAND CO.: near Bird Haven, 2½ mi. n. of Olney, May 10, 1910, *Ridgway* (US); Larchmound, Olney, May 20, 1919, *Ridgway 807* (G). WHITE CO.: wooded hillsides, Grayville, June 22, 1919, *Palmer 15575* (M). POPE CO.: rocky hillside woods, Golconda, June 5, 1919, *Palmer 15367* (M). JOHNSON CO.: rocky hillside woods, Vienna, Apr. 28, 1919, *Palmer 14984* (M). ALEXANDER CO.: low rich woods, Olive Branch, May 10, 1919, *Palmer 15098* (M). ST. CLAIR CO.: Carondelet, Sept. 4, 1891, *Douglass* (M).

MINNESOTA. HOUSTON CO.: sandy soil, hillside, Spring Grove, June 5, 1902, *Rosendahl 351* (Minn); Winnebago Valley, June 12, 1899, *Wheeler 184* (Minn). WINONA CO.: Winona, June, July, 1912, *Freiberg* (M); dry sandy soil and stony side of bluffs, without locality, June, 1886, *Holzinger* (Minn). WABASHA CO.: woods, Lake City, May, 1881, *Hammond 43* (Minn); near Lake City, June 14, 1883, *Manning* (Minn). OLMSTEAD CO.: Rochester, Lat. 44, June 17, 1902, *Ainslie 1040* (Minn). GOODHUE CO.: Cannon Falls, May, 1881, *Sandberg* (Minn). RAMSEY CO.: St. Paul, June 20, 1899, *ex herb. Moore & Moore* (RM). HENNEPIN CO.: rich woods, near Minneapolis, June, 1892, *Burglebaus* (Minn, MS); Lake Harriet, Sept. 15, 1896, *Heller* (Minn); Minneapolis, June 13, 1877, June, 1878, *Herrick* (Minn); Minneapolis, June, 1878, *Kassube* (Minn); Fort Snelling, June 9, 1891, *Mearns* (US); Fort Snelling Reservation, June 19, 1909, *Rosendahl 2132* (Minn); Minneapolis, June, 1895, *Sheldon* (Minn). CARVER CO.: Chaska, June, 1891, *Ballard 67, 69* (Minn). RICE CO.: Northfield, 1912, *without collector G. 139* (Minn). LE SUEUR CO.: Elysian, June, 1891, *Sheldon 41* (Minn); Elysian, June, 1891, *Taylor 34* (Minn). NICOLLET CO.: Middle Lake, June, 1892, *Ballard 969* (Minn). WASECA CO.: Janesville, June, 1891, *Taylor 118a, 262* (Minn). BLUE EARTH CO.: Madison Lake, June,

1891, *Sheldon* 116 (Minn). STEARNS CO.: St. Cloud, June, 1897, *Campbell* (FM, Minn). MEEKER CO.: Litchfield, June, 1892, *Frost* (Minn). KANDIYOHI CO.: Willmar, June, 1912, *without collector* 89 (Minn). ROSEAU CO.: Oak Point, July, 1894, *MacMillan & Sheldon* 1098 (Minn). POLK CO.: Crookston, Aug., 1900, *MacMillan & Skinner* (Minn). CLAY CO.: rich woods, Moorhead, June 18, 1929, *Solheim* 205 (RM). OTTERTAIL CO.: Battle Lake, Aug., 1892, *Sheldon* 3357 (Minn). JACKSON CO.: vicinity of Heron Lake, June 10, 1902, *Skinner* 45 (Minn). PIPESTONE CO.: Pipestone, June, 1895, July, 1896, *Menzel* (Minn). ROCK CO.: at base of mound, Luverne, Sept. 10, 1901, *Wheeler* 1068 (Minn).

IOWA. WINNESHIEK CO.: rich woods, without locality, June 18, 1895, *Fitzpatrick & Fitzpatrick* 2643 (G). FAYETTE CO.: wooded hillsides, Fayette, July, 1893, *Fink* (G); rocky hillside, without locality, June 28, 1894, *Fink* 572 (US). BLACKHAWK CO.: Snag Creek woods, June 14, 1929, *Burk* 343 (M); clay soil, Cedar Falls, July 7, 1926, *Pammel* 263 (G, M); sandy soil, woods and islands of Cedar River, Island Y.M.C.A. Camp, Cedar Falls, July 9, 1925, *Pammel* 663 (G). JOHNSON CO.: woods, without locality, June 13, 1900, *Fitzpatrick & Fitzpatrick* (D); Iowa City, *Hitchcock* (M). POWESHIEK CO.: Grinnell, 1886, *Norris* (M). VAN BUREN CO.: rich woods, Bentonsport, June, 1920, *Graves* 1719 (M); Stockport, June, 1925, *Graves* 2055 (M). DECATUR CO.: moist woods, Decatur, June 29, 1904, *Anderson* (RM); low rich woods, without locality, June 6, 1898, *Fitzpatrick & Fitzpatrick* (FM, RM). SHELBY CO.: without locality, May 30, 1894, *Fitzpatrick & Fitzpatrick* (M, MS). WOODBURY (?) CO.: ravines, "Sargeant's hill" [Sargeant Bluff?], June, 1853-54, *Hayden* (M).

MISSOURI. SCOTLAND CO.: woods, north side of Wyaconda River, near Azen, June 30, 1933, *Palmer & Steyermark* 40982 (M, NY); along North Fork of Fabius River, w. of Memphis, June 30, 1933, *Palmer & Steyermark* 41000, 41001 (M). MARION CO.: Hannibal, May, 1906, Aug. 1, 1914, June 20, 1915, *Davis* 1200, 3105, 6588 (M); Scipio, July 24, 1915, *Davis* 4775 (M); church-yard slopes, Withers Mill, July 14, 1917, *Davis* 7545 (M). SHELBY CO.: near Bethel, June 29, 1933, *Palmer & Steyermark* 40914 (M). MACON CO.: Ethel, June 12, 1915, *Bush* 7622 (M). LINN CO.: without locality, May 30, 1937, *Crookshanks* 15 (M). RALLS CO.: Ilasco, Aug. 20, 1911, *Davis* 987 (M); Bear Creek bluffs, near Oakwood, June 2, 1916, *Davis* 1290 (M); near New London, June 27, 1933, *Palmer & Steyermark* 40716 (M). PIKE CO.: Norris farm, near Eolia, Aug. 26, 1916, *Davis* (M, Minn). LINCOLN CO.: Silex, May 29, 1915, *Davis* (M). ST. CHARLES CO.: Gilmore, May 26, 1917, *Davis* 7372 (M). ST. LOUIS CO.: rich woods, Allenton, May 20, 1918, *Churchill* (G); Allenton, May 26, 1886, *Eggert* (M); Jefferson Barracks, *Eggert* (M); Ramona Park, June 8, 1907, *Fullgraf* (M); near St. Louis, June 20, 1892, *Glatfelter* (UM); Windsor Springs, July 1, 1890, *Hitchcock* (M); Jefferson Barracks, July 6, 1890, *Hitchcock* (M); Meramec Highlands, July 29, 1905, *Johnson* (M); Allenton, June 8, 1903, *Kellogg* (M); Allenton, June, 1902, *Letterman* (M, US); Allenton, Aug. 13, 1933, *Lodewyks* 27 (M); Creve Coeur Lake, July 20, 1894, *Misch* (M); Meramec Highlands, May 23, 1897, *Norton & Ferguson* (M); St. Louis, July, Aug., 1891, *Trelease* (M). FRANKLIN CO.: Gray Summit, May 19, 1928, *Greenman* 4545 (M); Gray Summit, May 25, 1927, *Kellogg* 830 (M); St. Albans, June 5, 1930, *Kellogg* 15144 (M); in shade, moist hillside, Pacific, May 15, 1921, *Payson* 2460 (RM). JEFFERSON CO.: in moist rich shady soil, Antonia, May 30, 1937, *Barkley* 1149 (M, WS); woods, near Victoria, Aug. 24, 1892, *Eggert* (M); Selma, May 30, 1923, *Greenman* 4283 (M); Victoria, Aug. 7, 1890, *Hitchcock* (M); Kinniswick, June 7, 1885, *Wislizenus* 414 (M). WASHINGTON CO.: woods, near Mineral Point, May 29, 1892, *Eggert* (M). PERRY CO.: 1 mi. n. of Menfro, July 30, 1934, *Steyermark* 14041 (M). MADISON CO.: Mine La Motte, May 19, 1927, *Greenman* (M). IRON CO.: along railroad, near Vulcan, May 6, 1908, *Smith* 311 (FM); woods, Des Arc, May 12, 1908, *Smith* 380 (FM); Ironton, June 18, 1897, *Savage & Stull* 197 (FM). WORTH CO.: 1 mi. s. of Denver, Aug. 30, 1934, *Steyermark* 15053 (M). GENTRY CO.: low woods, along East Fork of Grand River, 3 mi. n. w. of Albany, Aug. 29, 1934, *Steyermark* 15014 (M). ATCHISON CO.: Watson, June 1, 1894, *Bush* 527 (M). CALDWELL CO.: 6 mi. n. of Cowgill, Aug. 26, 1934, *Steyermark* 14884 (M). CLINTON CO.: 6 mi. s. of Cameron, Aug. 27, 1934, *Steyermark* 14918 (M). CLAY CO.: without locality, July 18, 1933, *Bush* 12690 (M). JACKSON

co.: Independence, June 7, 1894, *Bush* 533 (M); prairies, Lake City, June 2, 1915, *Bush* 7565 (G, M, NY, US); Courtney, June 7, 8, 17, 1917, *Bush* 7906 (M), 7906A (NY), 8000 (M, US), 8000A (NY, US), 8002 (M); Swope Park, June 9, 1917, *Hoffmann* (M). JOHNSON co.: rich woods, near Columbus, June 22, 1930, *Palmer* 36717a (M). CASS co.: without locality, June 9, 1864, *Broadhead* (M). COOPER co.: Otterville, May 19, 1936, *Bush* 15523 (M). MORGAN co.: low slopes, along Procter Creek, July 7, 1934, *Steyermark* 13194 (M). PHELPS co.: Jerome, May 28, 1914, *Kellogg* 537 (M). ST. CLAIR co.: Osceola, July 28, 1933, *Bush* 12804 (M). CEDAR co.: n. of Bear Creek P. O., July 16, 1934, *Steyermark* 13548 (M). GREENE co.: Springfield, June 7, 1903, *Standley* (US); vicinity of Springfield, June 15, 1907, *Standley* (US); along railroad, s. e. of Springfield, Aug. 29, 1911, *Standley* 8392 (US); thin woods, vicinity of Strafford, Aug. 27, 1912, *Standley* 9499 (US). JASPER co.: Webb City, June 14, 1903, *Palmer* 735 (M); low rich woods, Neck City, Aug. 16, 1919, *Palmer* 15872 (Farwell); Webb City, Aug. 18, 1919, *Palmer* 15922 (Farwell); near Reeds, June 2, 1924, *Palmer* 25259 (M). BARRY co.: Flat Creek, May 19, 1936, *Bush* 15513 (M).

ARKANSAS. CRAIGHEAD co.: Jonesboro to Lake City, July 5, 1927, *Demaree* 3582 (M). FULTON co.: Mammoth Spring, June 1, May 14, 1924, *Wheeler* 14, 37 (FM). FAULKNER co.: Arkansas River, 7 mi. w. of Conway, May 30, 1923, *Wheeler* 79 (FM). CARROLL co.: Eureka Springs, May 15, 1914, *Palmer* 5624 (M). WASHINGTON co.: near Farmington, May 4, 1925, *Palmer* 26087 (M).

LOUISIANA. NATCHITOCHE PARISH: sandy hillside woods, Chopin, April 21, 1915, *Palmer* 7335 (M, NY, US).

NORTH DAKOTA. RAMSAY co.: moist woods, Devils Lake, July 1, 1905, *Lunell* 286 (Minn). BENSON co.: thickets, Peninsula of Lake Ibsen, Aug. 15, 1906, *Lunell* 286, Aug. 27, 1909, 701 (Minn), Sept. 3, 1914, 1232 (Minn TYPE of *P. commutatum* var. *lineamentosum* Lunell, NY). BOTTINEAU co.: prairies, Willow City, June 20, 1889, *Lunell* (RM). MCHENRY co.: Towner July 21, 1908, *Lunell* (NY). WARD co.: rich alluvial soil, river bank near picnic grounds, Oak Park, Minot, June 21, 1929, Sept. 2, 1929, *Lakela* 173 (Minn). CASS co.: banks of Red River, Fargo, Sept. 29, 1933, *Nelson* & *Nelson* 1019 (RM). LAMOURE co.: open woods, Adrian, June 27, 1912, *Bergman* 1822 (Minn). MORTON co.: without locality, July 5, 1906, *Bell* 296 (M).

SOUTH DAKOTA. ROBERTS co.: rich woods, Coulee, July, 1922, *Over* 14332 (US). GRANT co.: Big Stone, Aug., 1894, *Williams* (RM). BROOKINGS co.: Lake Oakwood, *Griffiths* (M); shady banks, Lake Hendricks, June 11, 1898, *Hepner* (RM); damp woods, Oakwood, May 23, 1902, *Johnson* (M); Warren woods, Brookings, June 11, 1898, *Lawrence* (WS); Brookings, Aug., 1924, *Moore* 1562 (Minn); Lake Campbell, Aug., 1924, *Moore* 1569 (Minn). HANSON co.: Alexandria, May 11, 1911, *Weber* (UF). UNION co.: thickets, Brule Creek, June 27, 1921, *Over* 13682, 13683 (US). CLAY co.: woods, Vermillion, May 22, Aug. 1, 1911, *Visser* 4018 (FM, M), June 28, 1910, 4167 (M).

NEBRASKA. DIXON co.: Ponca, June 14, 1893, *Clements* 2545 (G, Minn, US). CEDAR co.: St. Helena, *Brubin* (M). CASS co.: South Bend, May 12, 1900, *Hedgcock* (M). LANCASTER co.: s. w. of Lincoln, June 5, 1900, *Hedgcock* (M); Lincoln, Aug., 1889, *Webber* (M, NY). GAGE co.: moist woods, Beatrice, June 13, 1899, *Washburn* (US). NUCKOLLS co.: without locality, July, Aug., 1899, *Hedgcock* (M). WEBSTER co.: Red Cloud, June 8, 1904, *Bates* 3212 (Minn). THOMAS co.: hillside, Middle Loup River, near Norway, June 22, 1893, *Rydberg* 1408 (US); dry hillside, near Plummer Ford, Dismal River, July 5, 1893, *Rydberg* 1483 (G, NY, US). LINCOLN co.: Hershey, June 11, 1903, *Mell* 98 (US).

KANSAS. CRAWFORD co.: 6 mi. s. e. of Pittsburg, June 21, 1929, *Rydberg* & *Imler* 165 (NY). RILEY co.: Prospect Hill, near Manhattan, Sept. 28, 1923, *Nelson* (M); Manhattan, Aug. 26, 1892, *Norton* (C); woods, without locality, 1896, *Norton* 834 (G, M, NY, RM, US); Manhattan, Aug. 19, 1892, *Thompson* (M). LYON co.: wooded hillsides, without locality, May 29, 1895, *Chamberlin* (WS). COWLEY co.: without locality, June, 1898, *White* (M).

OKLAHOMA. OTTAWA co.: moist woods, near Ottawa, Aug. 29, 1913, *Stevens* 2506 (G, Minn). ROGERS co.: Catoosa, May 14, 1895, *Bush* 1282 (M). OSAGE co.: on shady wooded creek bank, near Pawhuska, Aug. 9, 1913, *Stevens* 1999 (G, M, Minn, US).

PAYNE CO.: sandy wet soil, 2 mi. n. of Ripley, June 29, 1935, *Dillingham* (WVU). CREEK CO.: Sapulpa, July 27, 1894, *Bush* 578 (M). LOGAN CO.: shady hillside, Cimarron Bluffs, near Guthrie, June 14, 1914, *Stevens* 3292 (G). MCCURTAIN CO.: near Shawneetown, Aug. 13, 1853, *Bigelow* (US); Boggy Creek, Shawneetown, *Bigelow* (NY). MURRAY CO.: Platt National Park, Oct. 31, 1935, *Merrill & Hagan* 1691 (FM). COMANCHE CO.: vicinity of Fort Sill, May 20, 1916, *Clemens* 11532 (M, RM). COUNTY NOT DETERMINED: chiefly on the False Washita, between Fort Cobb and Fort Arbuckle, 1868, *Palmer* 325 (NY, US).

TEXAS. HARDIN CO.: $7\frac{3}{4}$ mi. w. of Silsbee, Village Creek, Oct. 6, 1934, *Cory* 11169 (G).

MEXICO. NUEVO LEON: Mesa Canyon, mountains near Monterrey, July, 1933, *Mueller & Mueller* 339 (G, FM).

UNIDENTIFIED SPECIES

Convallaria birta Bosc ex Poirét in Lamarck, *Encyc. Méth. Bot.* 4:369. 1797.

Polygonatum birtum Pursh, *Fl. Am. Sept.* 1:234. 1814.

No species conforming to the original description of *Convallaria birta* is known from North America.

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Accepted scientific names are in Roman type; synonyms, in *italics*; a new name and a new combination, in **bold face** type.

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